DREDGED MATERIAL RESEARCH PROGRAM

TECHNICAL REPORT D-77-35

MODELING OF ECOLOGICAL SUCCESSION AND PRODUCTION IN ESTUARINE MARSHES

by

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November 1977

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1. The technical report transmitted herewith represents the result of Work Unit 4A05 regarding the development and testing of a predictive model for marsh productivity and succession. This work unit was conducted as part of Task 4A (Marsh Development) of the Corps of Engineers' Dredged Material Research Program (DMRP). Task 4A is a part of the Habitat Development Project of the DMRP and is concerned with developing, testing, and evaluating the environmental, economic, and engineering feasibility of using dredged material as a substrate for marsh development.

2. The purpose of this work unit was to develop a simulation model of plant growth and succession on salt marshes. The model was created by identification of the biotic and physical factors that control plant growth and the measurement of these factors under field conditions. The model appears to have great potential for use in establishing criteria and specifications for salt marsh development; however, additional parameterization and verification will be required before the system becomes fully operational.

3. Work Unit 4A05 is one of several research efforts designed by the DMRP to accurately document marsh productivity and the factors which influence that productivity. Closely related work units are 4A04A1 and 4A04B, which address the productivity of minor marsh species along the Atlantic and Gulf coasts, respectively; 4A04A2, which deals with marsh plant substrate selectivity and underground biomass production; and 4A20, a less intensive effort that will provide a general evaluation of salt marsh productivity on the Pacific coast of the United States. Additional supportive and comparative data will be forthcoming with the final analysis of the results of field studies at Windmill Point, Virginia, (4A11); Buttermilk Sound, Georgia, (4A12); Apalachicola, Florida, (4A19); Bolivar Peninsula, Texas, (4A13); Pond No. 3, California, (4A18); and Miller Sands, Oregon, (4B05). Together these

research products provide the Corps with a comprehensive basis for sound management decisions regarding habitat development on dredged material and disposal in natural marsh habitats.

JOHN L. CANNON
Colonel, Corps of Engineers
Commander and Director

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Rapid disappearance and deterioration of wetlands as a consequence of increasing human utilization coupled with growing recognition by the scientific community of the ecological importance of these areas indicate the need to investigate ecologically sound alternatives for using dredged material. Three parallel studies were conducted with the development of a simulation model of plant growth and succession on a salt marsh being the ultimate objective. Field studies showed that Spartina alterniflora exhibited a strong

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20.   ABSTRACT (Continued).

positive correlation with the elevation and tidal inundations at the two major
study sites, Taskinas Creek and Bennett's Creek, in Virginia. S. alterniflora
showed a negative correlation with soil salinity and significant positive
correlation with available iron. Responses of S. patens and Distichlis
spicata were more variable, but where regular flooding occurred there was a
strong positive correlation with S. patens abundance and negative correlation
with D. spicata.

        Records from the continuous monitoring study reinforce the concept of
tidal inundation acting as a master variable. Power spectrum analysis of
continuous research of temperature and pH in the sediments revealed that in
the S. alterniflora zone the sediment surface temperature showed the major
power peak to be 0.089 cycle/hour, which is the tidal frequency for this area.
In the higher S. patens – D. spicata zone the frequency with the largest power
component is that of nearly 1 cycle/day corresponding to the input of solar
radiation. The analysis of pH data showed a large influence in the low S.
alterniflora at the tidal frequency but not in the high marsh.

        A model was developed which depicted plant growth and succession across
a transect. The model was driven by solar radiation, temperature, soil
salinity, and tidal inundation. The model showed plant growth controlled
primarily by tidal inundation, with influences felt from radiation and tem-
perature, but little influence due to salinity. The model appears to have
great utility for future use but presently is limited in application by
incomplete parameterizations.

EXECUTIVE SUMMARY

Rapid disappearance and deterioration of wetlands as a conse-
quence of increasing human utilization coupled with growing recogni-
tion by the scientific community of the ecological importance of these
areas indicate the need to investigate ecologically sound alternatives
for using dredged material. Attempts to recolonize disposal areas
after deposition have thus far met with mixed success. In attempting
to establish a desired community, two options are available: (1) create
environmental conditions favorable for the colonization of the desired
species, or (2) introduce a species that is compatible with the present
environmental conditions and allow natural succession to produce the
desired species or community. In order to achieve the desired ecosys-
tem by either of the two above approaches, the dominant controlling
forces on the communities must be known and described.

Three parallel studies were conducted with the development of a
simulation model of plant growth and succession on a salt marsh being
the ultimate objective. The first component was concerned with deter-
mining the biotic and chemical parameters present at a series of
marshes. The second component was concerned with obtaining continuous
records of several physical and chemical parameters within several
vegetation zones. The third component of the project was the development
of the simulation model.

Field studies showed that _Spartina alterniflora_ exhibited a
strong positive correlation with elevation and tidal inundations at the
two major study sites, Taskinas Creek and Bennett's Creek, in Virginia.

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S. alterniflora showed a negative correlation with soil salinity and significant positive correlation with available iron. Responses of S. patens and Distichlis spicata were more variable, but where regular flooding occurred there was a strong positive correlation with S. patens abundance and negative correlation with D. spicata.

Records from the continuous monitoring study reinforce the concept of tidal inundation acting as a master variable. Power spectrum analysis of continuous research of temperature and pH in the sediments revealed that in the S. alterniflora zone the sediment surface temperature showed the major power peak to be at 0.089 cycle/hour, which is the tidal frequency for this area. In the higher S. patens – D. spicata zone the frequency with the largest power component is that of nearly 1 cycle/day corresponding to the input of solar radiation. The analysis of pH data showed a large influence in the low S. alterniflora at the tidal frequency but not in the high marsh.

A model was developed which depicted plant growth and succession across a transect. The model was driven by solar radiation, temperature, soil salinity, and tidal inundation. The model showed plant growth controlled primarily by tidal inundation, with influences felt from radiation and temperature, but little influence due to salinity. The model appears to have great utility for future use but presently is limited in application by incomplete parameterizations.

PREFACE

This report presents the results of an investigation of factors influencing plant zonation and succession on salt marshes. The study was supported by the U. S. Army Engineer Waterways Experiment Station (WES), Habitat Development Project, Dredged Material Research Program, Vicksburg, Mississippi, under contract No. DACW39-73-C-0121 to the University of Virginia, Charlottesville, Virginia.

The project was directed by Joseph C. Zieman and William E. Odum of the Department of Environmental Sciences of the University of Virginia. Field Sampling and laboratory analysis were performed by Mark L. Gleason, Thomas G. Wolaver, Jeffrey E. Drifmeyer, and Michael B. Robblee.

The study was conducted under Dr. Kent Thornton, Contract Manager, and Dr. Hanley K. Smith, Habitat Development Project Manager, WES. The study was under the general supervision of Dr. John Harrison, Chief, Environmental Effects Laboratory, WES.

The Directors of WES during the study and the preparation of this report were COL G. H. Hilt, CE, and COL J. L. Cannon, CE. Technical Director was Mr. F. R. Brown.

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CONVERSION FACTORS, U. S. CUSTOMARY TO METRIC (SI) UNITS OF MEASUREMENT

The U. S. customary units of measurement used in this report can be converted to metric units as follows:

Multiply	By	To Obtain
microns	0.000001	meters
inches	2.54	centimeters
feet	0.3048	meters
acres	4046.856	square meters
pounds (force) per square inch	6894.757	pascals
miles (U. S. statute)	1.609344	kilometers

PART I: INTRODUCTION

1. In recent years the value of tidal wetland as nursery areas, as
buffers against shoreline erosion, and as sources of energy for shell-
fish and commercial and sport fisheries has become widely recognized
(Schelske and Odum, 1971; Teal, 1962; Odum and de la Cruz, 1967;
Cooper, 1969; Williams and Murdoch, 1969; Keefe, 1972; Odum, Zieman
and Heald, 1972). Estuaries are among the most productive natural eco-
systems on earth, and serve as vital recreational, transportation,
industrial, commercial, and population sites (Allen, 1964).

2. With accelerating human uses of estuaries have come altera-
tions and modifications of the natural ecosystem. Chief among these
is dredging and dredged material disposal. Dredging and filling has
altered over 7 percent of the total estuarine habitat in the United
States; 570,000 out of 8 million acres[*] have been lost (Marshall, D. E.,
1970). Along the northeastern Atlantic coast, dredging is the predominant
means of wetland alteration (Marshall, D. E., 1970; Schmidt, 1966). For
example, of the 45,000 acres of wetlands between Maine and Delaware
destroyed from 1955 to 1964, fully one-third was lost to dredged mate-
rial disposal (Schmidt, 1966). During this same period, South Carolina
lost 10 percent of its total wetland acreage to dredged material dis-
posal, while Florida filled 60,000 acres, or 7.5 percent, of its most
important estuarine areas (Teal and Teal, 1969; Marshall, D. E., 1970).
Along the Gulf Coast dredging and fill operations have also impacted

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[*] A table of factors for converting U.S. customary units of measure-
ment to metric (SI) units can be found on page 12.

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estuaries; Texas lost 55,000 acres of shallow marine bay habitat and 23,000 acres of brackish marsh (Chapman, 1967).

3. The biological effects of dredging and disposal are often deleterious, as has been discussed by Thompson, 1961; Chapman, 1967; and Odum, 1970. Excessive sedimentation, increased turbidity and alteration of circulation patterns may adversely affect benthic populations, photosynthetic activity, and energy flow. For example in Boca Ciega Bay, Florida, 3,500 acres of dredged material deposition severely reduced annual production of seagrasses (by 25,851 metric tons), infauna (by 1,091 metric tons), and fisheries (by 73 metric tons) (Marshall, D. E., 1970). While not an exhaustive list, the above show that dredging operations have the potential to alter significant portions of existing wetlands.

4. Rapid disappearance and deterioration of wetlands as a consequence of burgeoning human utilization, coupled with growing recognition by the scientific community of the ecological importance of these areas, indicate the need to investigate ecologically sound alternatives for using dredged material. In particular, the possibility of using dredged material to build new marshes has been suggested repeatedly (Smith, 1942; Larimer, 1968; Teal and Teal, 1969; Woodhouse et al., 1972; Connecticut State Board of Fisheries and Game, undated).

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PART II: PROJECT CONCEPT AND DEVELOPMENT

5. Understanding of marsh plant physiology and ecology is presently insufficient to offer design criteria for dredged material disposal that would facilitate rapid recolonization of marshes. Attempts to recolonize disposal areas after deposition have met with mixed success (Windom, 1972; Woodhouse et al., 1972; Vittor,1971; Larimer, 1968). Ecological succession is an orderly process of community development that involves changes in species composition and community processes over time. In marsh areas, the sequence of plant species is well documented, but the processes and driving forces behind these changes are poorly understood. As one community (an assemblage of populations within a given area) grows, it modifies its environment, creating conditions favorable for a subsequent community. The environment of a mature community may resemble that of its early successional predecessors only slightly--a fact that is often overlooked by those who attempt to establish particular communities artificially.

6. In attempting to establish a desired community, two options are available: (1) create the environmental conditions favorable for the colonization of a desired species, or (2) introduce a species that is compatible with the present environmental conditions and allow natural succession to produce the desired species or community. In order to achieve the desired ecosystem by either of the above approaches, the dominant controlling forces on the communities must be known and described. In addition, the second procedure requires knowledge of the direction in which succession will proceed.

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7. A comprehensive understanding of the development of estuarine marshes requires knowledge of the physical and chemical parameters affecting marsh plants. The ways in which sediment characteristics such as organic content, sediment texture, and mineralogy condition the habitat of marsh plants have been elucidated by previous workers (Richards, 1954; Fleming and Alexander, 1961; Windom, 1972).

8. According to the classification of Sanders (1969), marsh ecosystems are controlled primarily by physical factors. The ecological stresses imposed by the broad variability of physical factors reduce the relative influence of biotic competition as a control of species distribution. Since relatively few plants and animals can withstand rapid tidal, salinity, and temperature fluctuations, species diversity in tidal marshes tends to be low. In a study of saline and brackish marshes in Louisiana, Chabreck (1972) found that in the low marsh zone, dominated by Spartina alterniflora and strongly influenced by tides, three species accounted for over 70 percent of the higher plants encountered.

9. The tools of simulation modeling which are beginning to come into use in environmental studies offer great potential for the future (Patten, 1971, 1972). However, most attempts to apply modeling techniques to ecological problems have suffered from several crucial deficiencies. First, to be a useful decision tool, a model must be designed to answer specific questions. Thus far, few ecological models have been so structured; rather, most attempt to describe the "normal behavior" of a particular system, and have thus been largely

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descriptive. Second, to properly develop a simulation model of an eco-
system it is necessary to understand component interactions and the bio-
logical theory behind these interactions. Third, for proper implementa-
tion the best conceived model still requires reliable dynamic informa-
tion, such as flux rates. This information has seldom been measured in
the past and generally is not available in the literature. For best
results, the input parameters should be measured simultaneously and con-
tinuously.

10. At present the difficulty of collecting accurate dynamic
field data and ignorance of the biological functioning of the marsh eco-
system are more serious hindrances to ecological modeling than misappli-
cations of systems analysis and modeling techniques. One of the
toughest problems faced by ecological modelers today is in the gather-
ing of accurate environmental data at closely spaced intervals of time.
For years, physical scientists have recorded data at exceptionally high
acquisition rates; biologists, however, have been restricted to sam-
pling field sites on a weekly or monthly basis, distorting interpreta-
tion of environmental parameters that vary widely and rapidly.

11. Simulation modeling is essentially a cyclical process cen-
tered around the design and conceptualization of the model, the formu-
lation process, the parameterization of this model, and field studies
to verify the model. Following the completion of one cycle, the informa-
tion gained is used to modify the original concept and resulting model.
The process can be repeated until satisfactory results are produced.

12. The ultimate objective of this project was to produce an

ecological simulation model capable of predicting vegetation succession on marshes and dredged material islands. Three parallel studies were pursued. The first component was concerned with determining the biotic and chemical parameters in a series of marshes. The objectives were to determine the range of selected environmental parameters that dominant species of marsh plants tolerate, and second to determine the seasonal variation of selected physicochemical parameters and the response of certain biotic compounds. A series of marshes from New Jersey to Georgia were visited and surveyed, but intensive effort was concentrated at two sites in Virginia. The results of this study are discussed in Part V.

13. The second study was concerned with obtaining continuous records of several physical and chemical parameters within several vegetative zones. The objective of this study was to characterize the magnitude of variation of edaphic factors in the major marsh communities. This involved the development of a continuous recording data-monitoring system described in Appendix A and the data and results are discussed in Part VI.

14. The third study of the project was the development of a simulation model of plant growth and succession on the marsh. The initial models were developed based on information available in the literature on the functioning of estuarine salt marshes. As the project progressed, information was added from field studies and contact with other scientists in the field. The latter input was aided by several meetings on marsh growth and reclamation at the Waterways

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Experiment Station, Vicksburg, Mississippi. Part VII contains the

development of the marsh succession model.

PART III: STUDY SITES

General Description

15. Field research was conducted intensively at two sites in Virginia as described below. In addition, surveys were conducted at a variety of marshes from New Jersey to Georgia. The data from the marsh surveys are presented in Appendix C.

16. Taskinas Creek Marsh is situated adjacent to the York River (lat. $37^{\circ}25'$, long. $76^{\circ}43'$), 16 km southeast of the city of West Point. The marsh and much of its watershed are included within York River State Park (Figure 1). The second marsh site is located on the east bank of Bennett's Creek, a tributary of the Nansemond River, about 300 m south of U.S. Route 17 (lat. $36^{\circ}51'$, long. $76^{\circ}28'30''$), 8 km west of Portsmouth. The marsh and adjacent uplands are privately owned.

17. Although they are approximately 60 km apart, Taskinas Creek Marsh and Bennett's Creek Marsh are alike in several respects. Both are small (less than 37 ha) pocket marshes adjoining the tidal tributaries of Chesapeake Bay. Their average tidal range (approximately 1 m) differs by less than 5 cm. Salinity of the creek water ranges from zero to approximately 15 percent at both sites. The distribution of vegetational communities is also similar. Spartina alterniflora dominates the lower margin of each marsh along the creek banks while a Spartina patens - Distichlis spicata association occupies the adjacent high marsh zone. Scirpus olney, and Scirpus robustus predominate where the marsh borders the uplands. The average width of each marsh
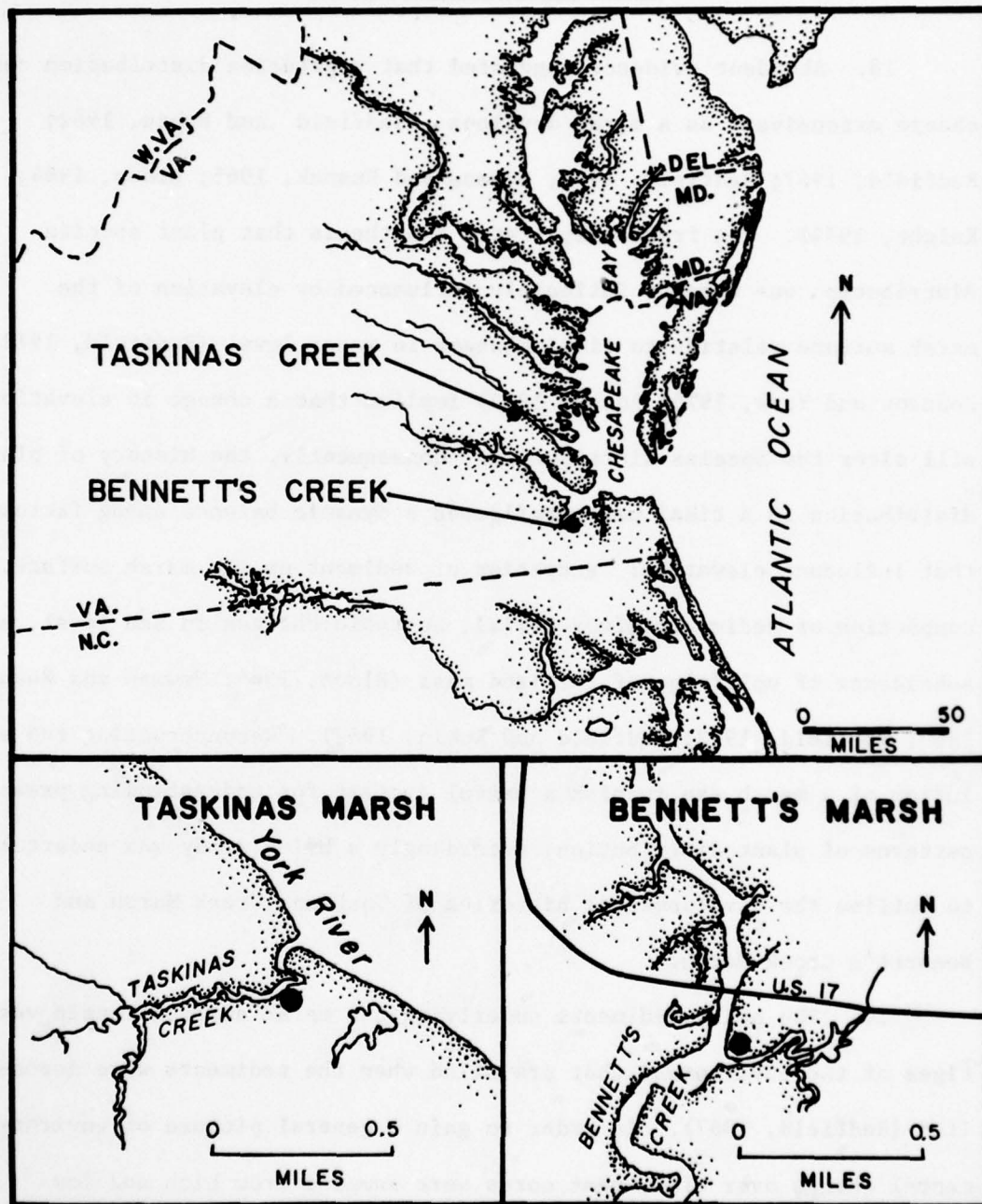
Figure 1. Location map indicating intensive study sites on the James and York Rivers.

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from creek bank to upland is approximately 100 meters.

Marsh Development History

18.   Abundant evidence suggested that vegetation distribution can change extensively as a marsh develops (Redfield and Rubin, 1962; Redfield, 1967; Redfield, 1972; Newman and Rusnak, 1965; Bloom, 1964; Knight, 1934). The frequently stated hypothesis that plant species distribution was somehow intimately influenced by elevation of the marsh surface relative to tidal changes in water level (Redfield, 1972; Johnson and York, 1915; Adams, 1963) implied that a change in elevation will alter the species distribution. Consequently, the history of plant distribution in a tidal marsh reflected a dynamic balance among factors that influence elevation: accretion of sediment on the marsh surface, compaction of sediments after burial, eustatic changes in sea level, and subsidence of uplifting of the land mass (Bloom, 1964; Newman and Rusnak, 1965; Redfield, 1972; Redfield and Rubin, 1962). Reconstructing the evolution of a marsh can furnish a useful context for understanding present patterns of plant distribution; accordingly a brief study was undertaken to outline the developmental histories of Taskinas Creek Marsh and Bennett's Creek Marsh.

19.   The peaty sediments underlying the marsh surface retain vestiges of the environment that prevailed when the sediments were deposited (Redfield, 1967). In order to gain a general picture of environmental change over time, peat cores were sampled from high and low marsh stations at each marsh, using an Oakfield Apparatus Company

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sectioned peat corer, to a maximum depth of 8.5 m. Sixteen-centimeter core sections were retained at 1.25-m depth intervals for the following laboratory analyses: percent moisture, percent organic matter, and plant species identification.

20. Core sections were analyzed for moisture and organic matter as outlined under "Laboratory Procedures" in Part IV. Subsamples of each section were washed through three sediment screens, of mesh sizes 2 mm, 250 μm, and 63 μm, respectively. The fraction retained on each screen was examined under a dissecting microscope; when possible, root and stem remains were identified by species. Each fraction was also described qualitatively, noting abundance of organic matter, presence of foraminiferan tests, type of inorganic sediment, and other observable features.

21. Approximate stratigraphic sequences in each marsh have been reconstructed from the data. Figure 2 depicts cross sections on low marsh to high marsh transects at Taskinas Creek Marsh and Bennett's Creek Marsh, respectively. Solid-line borders between adjacent strata connect points for which data exist; dashed lines represent more speculative extrapolations.

22. The deepest stratum sampled at Taskinas Marsh (Figure 2) appeared to be sedge peat, characterized by sparsely scattered sedge stems. Overlying the sedge peat was a relatively thick wedge of fine-textured clay silt, nearly devoid of identifiable detritus particles. Above the mud layer was a thick wedge of dense, fibrous high marsh peat composed predominantly of S. patens and D. spicata rhizome remains,

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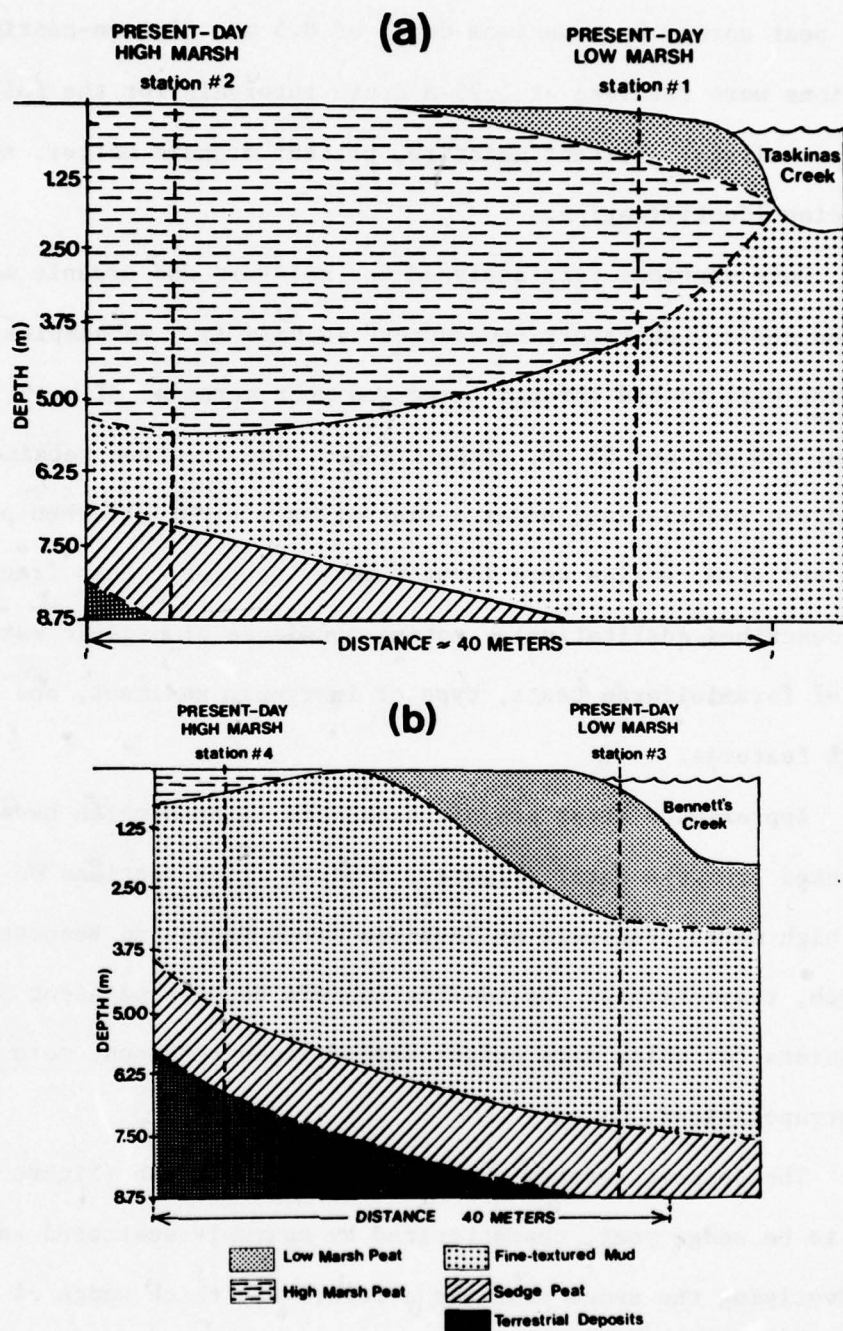
Figure 2. Cross section of sediment at Taskinas Creek (a)
and Bennett's Creek (b).

which extended uninterrupted to the marsh surface in the present-day high marsh. The most recent deposit was a relatively shallow (.7-1.0 m) lens of low marsh (S. alterniflora) peat covering the modern intertidal zone.

23. The stratigraphic sequence at Bennett's Marsh (Figure 2) was similar to the Taskinas profile, but with several important distinctions. Terrestrial sediments found at a depth of 6.8 m at station #4 indicated that the total thickness of marsh sediments may be considerably less than at Taskinas Creek--at least 1.9 m less. As at Taskinas Marsh, a layer of sedge remains was covered by a thick deposit of silty clay. However, low marsh deposits originated considerably deeper at Bennett's than at Taskinas, while high marsh peat at Bennett's that underlaid the modern high marsh surface was comparatively shallow (less than 0.6 m).

24. Lacking radiocarbon analyses of the peat samples, it was difficult to accurately establish the age of each stratum. Nevertheless, a general sequence of events was deduced by the principle of superposition (Leet and Judson, 1965).

25. Scattered studies of marshes bordering the East Coast of the United States suggested that contemporary marshes were of relatively recent origin. Bloom (1964) estimated a maximum age of approximately 7000 years before present (B.P.) for peat at the basement of a Connecticut salt marsh. Redfield's (1967, 1972) Cape Cod marsh dates back to 4000 years B.P., while the Wachapreague Marshes of Virginia's eastern shore appeared about 5000 years ago (Newman and Rusnak, 1965). It seemed reasonable, then, to infer that Taskinas Creek Marsh and Bennett's Creek Marsh originated within the last 4000 to 7000 years.

26. Based on core samples, the earliest macrophyte community at both marshes was apparently a brackish-water association characterized by sedges such as Scirpus. Bloom (1964) found a similar association in Connecticut marsh deposits. These early sedge marshes may have formed as narrow fringes separating the uplands from adjacent shallow bays. As sea level rose relative to the land, the fringing marshes continued to colonize the borders of the drowning uplands, while their seaward edges were reclaimed by the bays. Even today, the most abundant stands of Scirpus in Virginia salt marshes congregate along the upland margins. The association of a sedge zone fringing shallow bays has also been identified in Connecticut (Bloom, 1964), and elsewhere in Virginia (Newman and Rusnak, 1965).

27. The histories of Taskinas Marsh and Bennett's Marsh appeared to diverge with the initiation of a high marsh (S. patens and D. spicata) community at Taskinas, at a maximum depth of about 5.5 m below the present marsh surface. The data suggested that the transition from shallow bay mud to fibrous high marsh peat occurred relatively rapidly, perhaps even without an intervening low marsh stage (Redfield, 1972). Expansion of the high marsh may have coincided with the slow-down in rate of relative sea level rise that occurred along the East Coast around 2000-3000 years B.P., facilitating uplift of the marsh surface by sediment accretion (Redfield and Rubin, 1962; Newman and Rusnak, 1965; Bloom, 1964). The high marsh community spread across Taskinas Marsh, until the relatively recent appearance of S. alterniflora along the creek banks. Organic remains in the upper 0.9 m of

sediment indicated progressive expansion of this low marsh species rear-
ward across previous high marsh. Furthermore, Taskinas high marsh was
dotted with Iva frutescens, a shrub generally associated with a more
elevated habitat (Kurz and Wagner, 1957). Almost all of the I.
frutescens were dead. Coupled with the invasion of S. alterniflora
over the high marsh, these observations suggested that Taskinas Marsh
is presently undergoing a drowning phase; that is, the rise in relative
sea level is outstripping the vertical accretion of sediment, and retro-
gressive succession (Kurz and Wagner, 1957) appears to be occurring.

28. The mud stratum at Bennett's Marsh extended upward consider-
ably closer to the surface than at Taskinas Marsh. Although relative
ages of similar strata in each marsh could not be determined without
radio-carbon techniques, it seemed plausible that an open-water environ-
ment persisted until more recently at Bennett's Marsh, particularly in
the zones now occupied by high marsh species.

29. It appeared that a S. alterniflora community occupied the
intertidal zone at Bennett's long before a S. patens - D. spicata
association became established, since the high marsh peat layer is much
shallower than the low marsh peat (Figure 2). The presence of low
marsh and high marsh associations above the mud stratum suggested that
Bennett's Marsh has recently been undergoing an accreting phase; that
is, the vertical accumulation of sediment is surpassing the rise in
relative sea level. However, the data were insufficient to indicate
whether high marsh is now succeeding low marsh, or vice versa, or
whether the balance is stable.

30. In summary, the marsh stratigraphy investigation afforded the following perceptions:

(a) The development of Taskinas Marsh and Bennett's Marsh paralleled the general patterns outlined for other East Coast salt marshes (Redfield, 1967, 1972; Newman and Rusnak, 1965; Bloom, 1964; Hill and Shearin, 1970).

(b) Taskinas Marsh is presently undergoing a drowning phase, as sea level has risen relative to the surface of the marsh.

(c) Bennett's Marsh has recently been experiencing an accreting episode; i.e., the marsh surface has been elevated relative to sea level.

PART IV: METHODS

Field Procedures

31. After the results of preliminary studies were evaluated, a final transect design was adopted at the two intensive study sites, Taskinas Creek and Bennett's Creek. Three parallel belt transects were established in each marsh, extending across the ecotone from low marsh to high marsh. The transects (Figure 3) were 8 m longer at Bennett's Marsh than at Taskinas Marsh, and thereby encompassed two more sample zones in order to accommodate Bennett's broader distribution of vegetative zones.

32. Within each transect were equidistant "sample zones", 4-m x 1-m areas from which all plant and sediment samples were taken (Figure 3). Samples were gathered randomly within each zone by means of randomized assignment of numbers of the four adjacent $1-m^2$ quadrats in each sampling zone.

33. Plant samples and sediment cores were taken at four times during the spring and summer of 1975: 5-7 April, 29-30 May, 21 July, and 13 September. On each occasion, a single plant sample (shoots only) and three sediment cores were taken from each sample zone. Quadrats harvested were $0.1 \ m^2$ in zones where S. alterniflora appeared to be prevalent, and $0.04 \ m^2$ where S. patens and D. spicata predominated. Cores were taken with a brass coring apparatus (6.35 cm i.d.) and were extruded and frozen immediately.

34. Plant growth indices (stem biomass, height, density per m^2) and plant-available nutrient concentrations in sediments (NH_3, PO_4, Mn,

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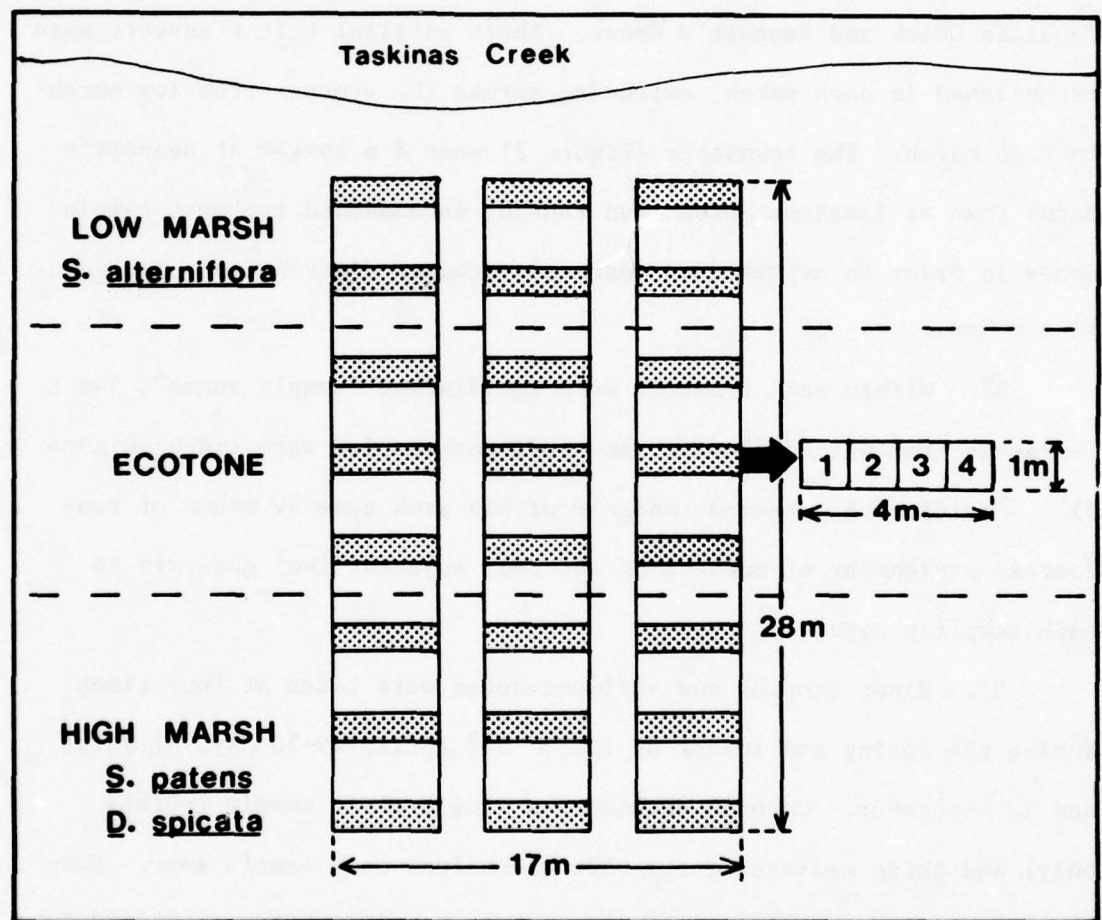
Figure 3. Experimental plot design at intensive study sites.

Ca, and Mg) were measured at all four sampling periods mentioned above. Two environmental factors were determined for a single sampling period only--organic matter content of sediments (21 July) and interstitial salinity (13 September).

35. Relative elevations of all sample sites were determined with a transit, plane table, and stadia rod on 2 July 1975. Elevations of Taskinas Marsh were rechecked on 9 September. Because no U.S.G.S. elevation bench marks were available for reference, a Mean Low Water datum for both creeks was established from tide height estimates published by the National Ocean Survey (U.S. Dept. of Commerce, 1974). The elevation of the creek surface at slack low water was measured relative to the sample zones, then corrected for departure from true mean low water as gauged at nearby NOAA tide stations. Slack low water level was surveyed at both creeks on 14 November 1975, a day of minimal wind activity, and rechecked during similar wind conditions at Taskinas Creek on 28 February 1976.

Laboratory Procedures

Plant samples

36. All live stems were separated by species and all dead stems were also grouped together. The number of live stems of each species was counted, and stem height was measured to the nearest centimeter for subsamples of ten stems per species. Live standing crop data for each species and total standing dead were obtained by drying grass samples in a drying oven for 48 hours at 105°C. Dried samples were weighed to ± 0.1 gram on a Mettler model P1200N top-loading balance.

31

Sediment cores

37. Analyses at the intensive sites were confined to the upper
20 cm of the sediment since none of the major plant species present
extends its roots significantly below that level. (Valiela and Teal,
1973; Broome et al., 1973). Soil subsamples were combined with a weak
acid extractant solution (Nelson et al., 1953), homogenized in a
blender, and filtered to obtain samples for nutrient analyses. Addi-
tional subsamples were ashed in a muffle furnace to determine organic
content of soils (see Appendix A for details of procedures).

Nutrient analysis

38. Concentrations of iron, manganese, calcium, and magnesium
in filtered samples were measured in a Varian Atomic Absorption Spectro-
photometer (model AA-5R). Sample intake was regulated by a Technicon
Sampler II automatic sampling apparatus, and data were recorded as peak
heights on a Varian model A-25 strip chart recorder. Calcium and mag-
nesium were run at 60 samples per hour using the Technicon proportion-
ing pump to add and mix one ml of $SrCl_2$ (5,000 ppm) to each ml of mag-
nesium and calcium sample.

39. Phosphate analyses were conducted on a Technicon Auto-
Analyzer; a combined reagent (0.18 M ammonium molybdate + .011 M ammon-
ium metavandate) was used (adapted from Steckel and Flannery, 1966).
The Sampler was set at 40 samples per hour, and peak heights recorded
on a Technicon "Recording System" strip chart. Duplicate determina-
tions were performed on all the foregoing automated analyses of each
sample.

32

40.   Ammonia concentrations were measured with an Orion model 95-10 ammonia electrode and an Orion model 401 specific ion meter.   Two ml of 10 M NaOH were added to 20 ml of constantly stirred sample solution to obtain a pH of approximately 11.00; after equilibration, ammonia concentration was measured to ± 0.1 ppm.

PART V: FIELD STUDY RESULTS AT INTENSIVE SITES

Habitat Factors

Vegetation

41. Four species of macrophytic phanerogams were encountered at
both study sites: S. alterniflora, S. patens, D. spicata, and Aster
tenuifolius (Figure 4). S. alterniflora predominated in the low marsh
zone fringing the tidal creeks, and S. patens and D. spicata occupied
adjacent high marsh areas. All three species inhabited the ecotone sep-
arating the zones, in varying proportions. A. tenuifolius, a minor
constituent throughout, occurred most frequently in the low marsh and
ecotone.

42. Seasonal data for live standing crop, standing dead, stem
density, and stem height of all species were condensed into annual sum-
mary values (Figures 5-9). Because of its relative scarcity, A. tenui-
folius was omitted from the summaries. Maximum live standing crop of
the three major species was graphed for Taskinas Marsh (Figure 5a) and
Bennett's Marsh (Figure 5b). At both sites, standing crop of S. altern-
iflora generally declined from the low marsh toward the high marsh
(left to right on the graphs). Maximum values occurred in the sample
zones closest to the creeks. S. patens live standing crop exceeded
D. spicata over most of their common range at both sites, although S.
patens decreased both landward and seaward from peak values. Miller
and Egler (1950) identified the S. patens - D. spicata association in
Connecticut tidal marshes; they termed the species "ecological

(a) TASKINAS MARSH

LOW MARSH   HIGH MARSH

S. patens

D. spicata

A. tenuifolius

S. alterniflora

distance = 28m

1 2 3 4 5 6 7 8

(b) BENNETT'S MARSH

LOW MARSH   HIGH MARSH

S. patens

D. spicata

A. tenuifolius

S. alterniflora

distance = 36 m

1 2 3 4 5 6 7 8 9 10
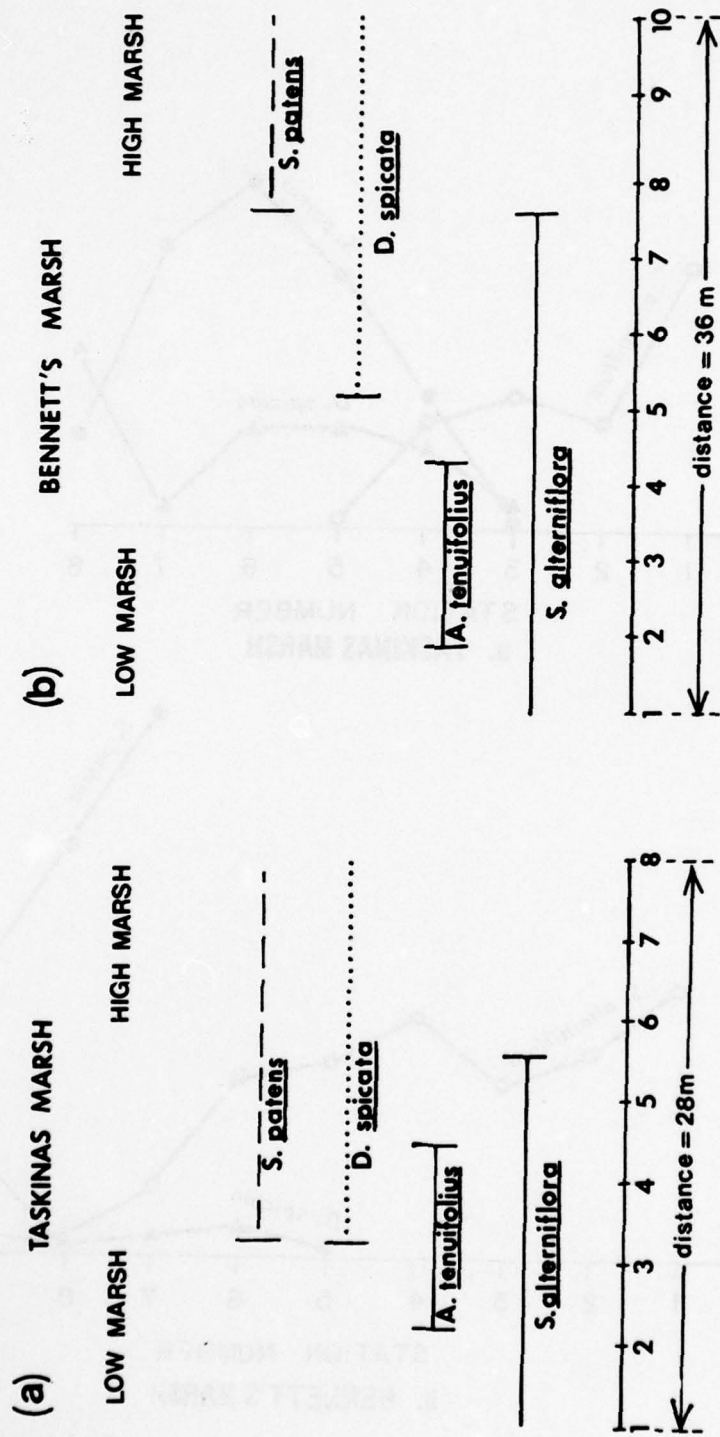
Figure 4. Ranges of plant species across transects at Taskinas Marsh and Bennett's Marsh.
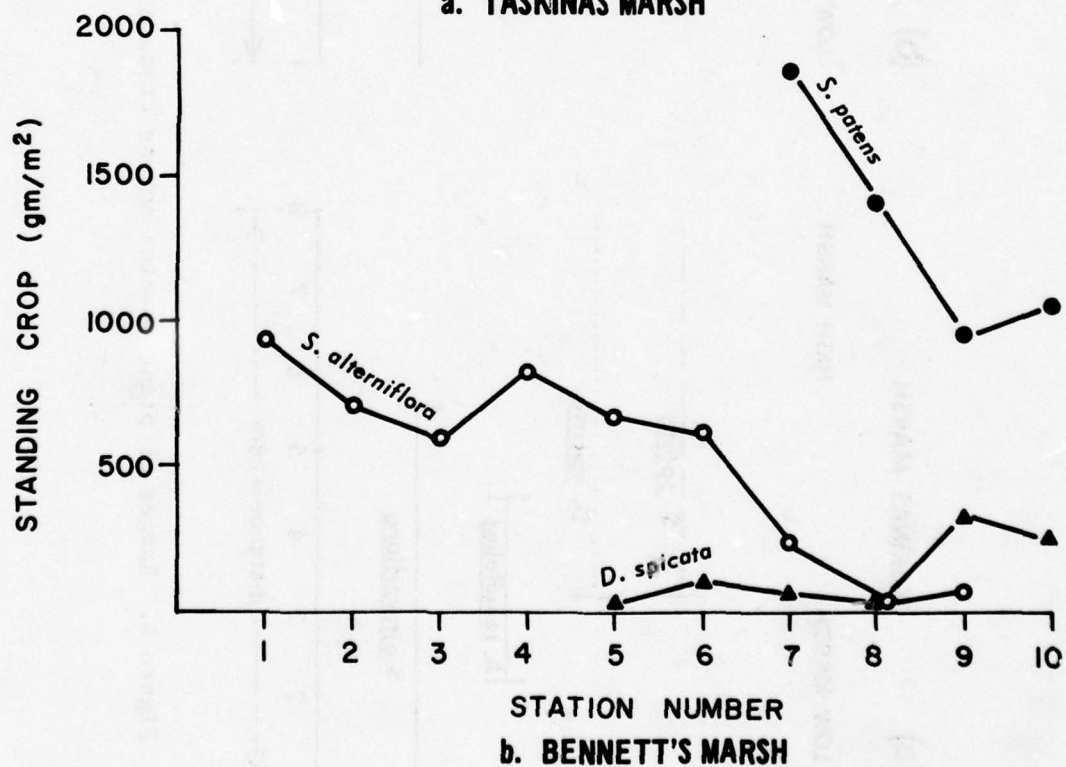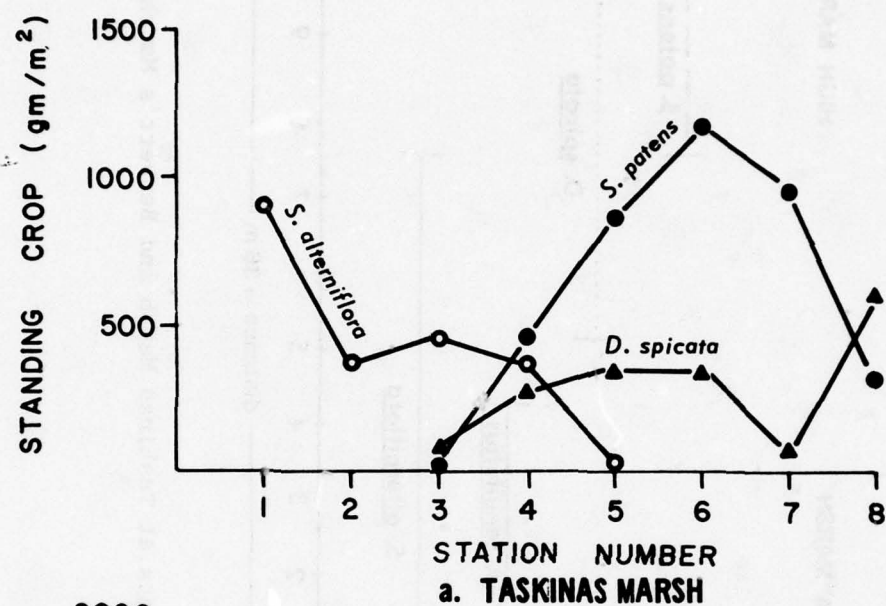
Figure 5. Maximum values for live standing crop at Taskinas Marsh (upper) and Bennett's Marsh (lower).

36

equivalents", while affirming that S. patens is usually dominant where they occur together. However, D. spicata surpassed S. patens along the seaward margin of their common range at Taskinas; indeed, at Bennett's Marsh, S. patens was entirely absent from sample zone 5, the seaward limit of D. spicata growth (Figure 5).

43. It is noteworthy that the largest standing crop values of S. patens exceeded those of S. alterniflora at both marshes--a reversal of the pattern reported from many other Virginia marshes (Keefe, 1972).

44. The spatial distribution of total standing dead material (Figure 6) is interesting for several reasons:

a) Accumulation of standing dead is considerably greater in the high marsh zone (S. patens, D. spicata) than in the low marsh (S. alterniflora).

b) The landward edge of the ecotone, adjoining the high marsh community, is marked by an abrupt change in the amount of standing dead.

c) The ratio of live standing crop to dead standing crop (L/D) in both low marsh and high marsh zones was considerably higher at Bennett's than at Taskinas. Since L/D ratios are considered to vary directly with the amount of tidal inundation that a marsh receives (Keefe and Boynton, 1973; Mendelssohn, 1973), Bennett's Marsh evidently has experienced more inundation than Taskinas Marsh. Predicted inundation values (discussed below) bolster this contention.

45. Data from July and September sampling periods (around the end of the growing season in Virginia marshes) were combined to yield
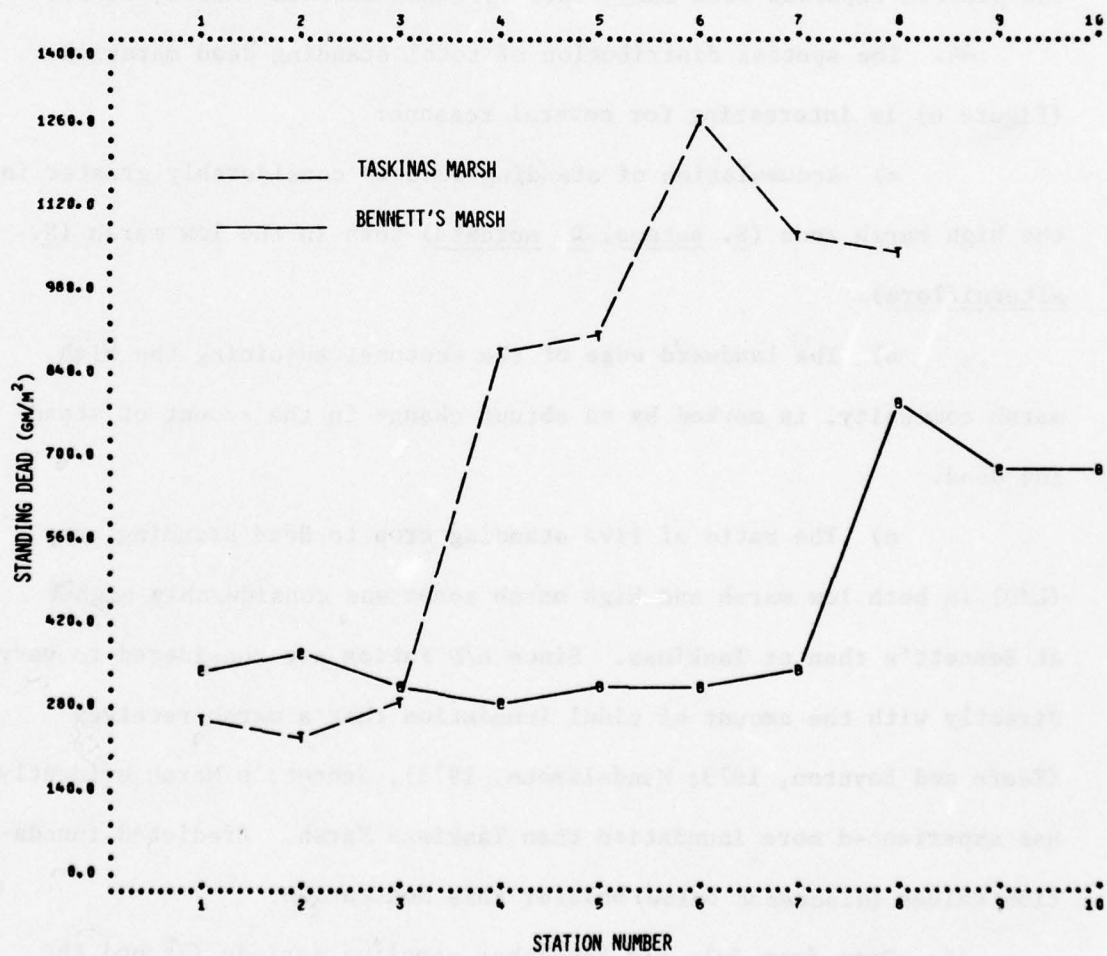
Figure 6. Maximum values for standing dead crop at Taskinas Marsh and Bennett's Marsh.

average maximum values for stem density and stem height. These

averages were adopted to approximate the maximum standing crop of the

plants and to reduce the amount of variability in the data.

46. The trend of spatial variation in stem density was similar

in both marshes (Figures 7 and 8); stem density reached a maximum in the

middle of the S. alterniflora range, followed by a precipitous decrease

at the ecotone. Comparison with Figure 5 indicated that maximum stand-

ing crop was not strictly coincident with maximum stem density, although

their patterns of fluctuation were qualitatively similar. Stem densi-

ties for the S. patens - D. spicata association (Figure 8) also

resembled the respective standing crop trends (Figure 5). In both

marshes, D. spicata exhibited its highest standing crop and stem density

values at the landward extremes of the transects.

47. Stem heights (Figure 9), like stem densities, represented

averages of July and September data. S. alterniflora steadily declined

in height rearward; the zone closest to the creek possessed both the

tallest stems and the largest standing crop values. While S. patens

and D. spicata were similar in stem height, S. patens was slightly

taller over most of their common range. Following the trend for

standing crop and stem density, D. spicata was taller than S. patens at

the seaward margin of the ecotone at Taskinas Marsh.

Elevation

48. Profiles of average elevation at Taskinas Marsh and Bennett's

Marsh (Figure 10), following the transects from low marsh (on the left)

to high marsh (on the right), offer several contrasts:

39
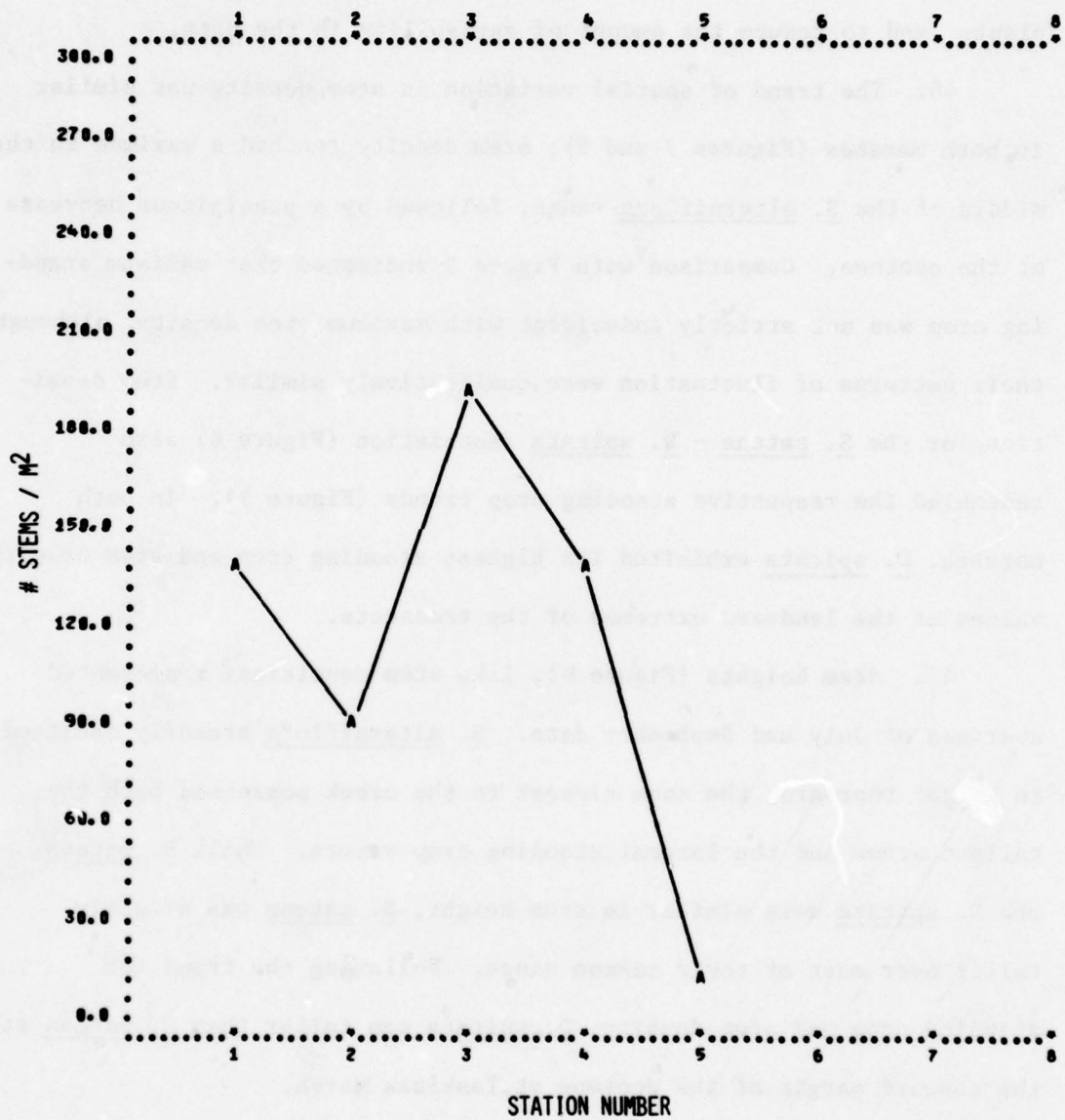
a. Taskinas Marsh

Figure 7. Maximum values for stem density of _Spartina alterniflora_ at Taskinas and Bennett's Marsh (sheet 1 of 2).
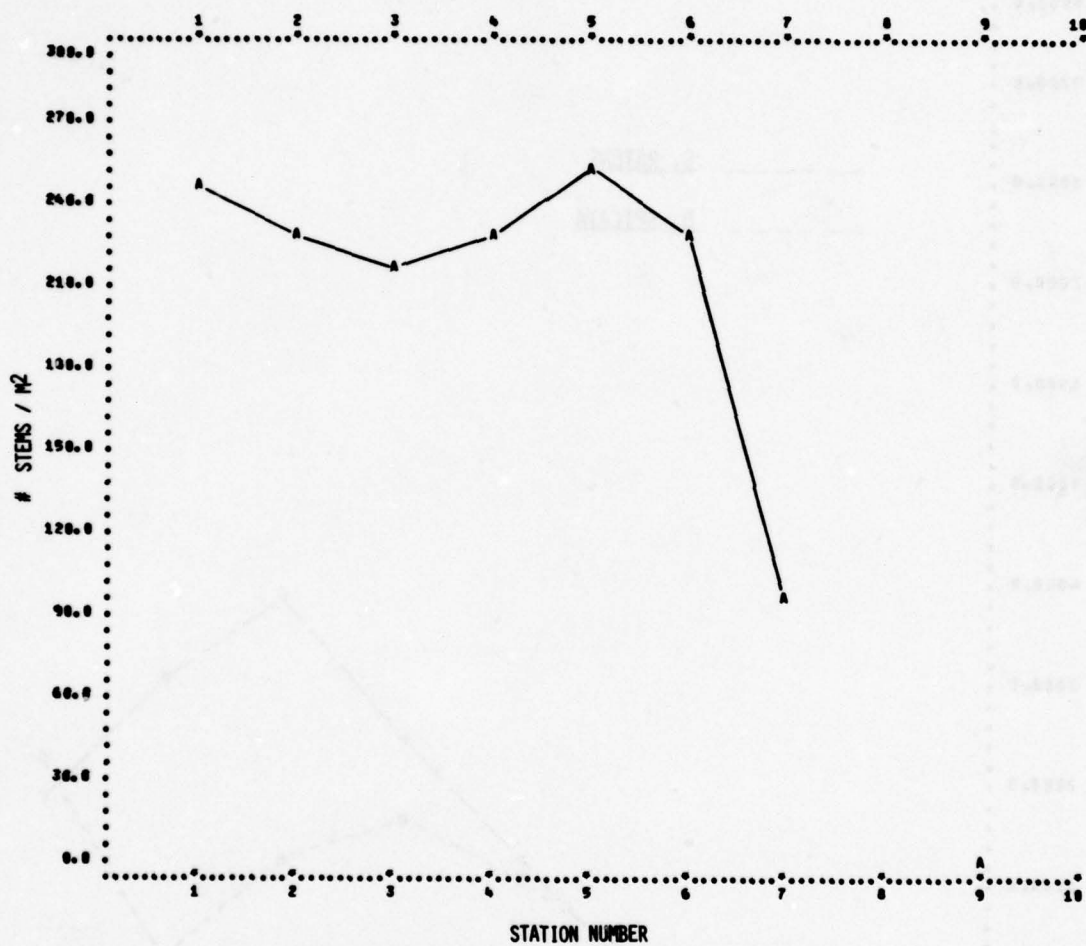
b. Bennett's Marsh

Figure 7 (sheet 2 of 2).
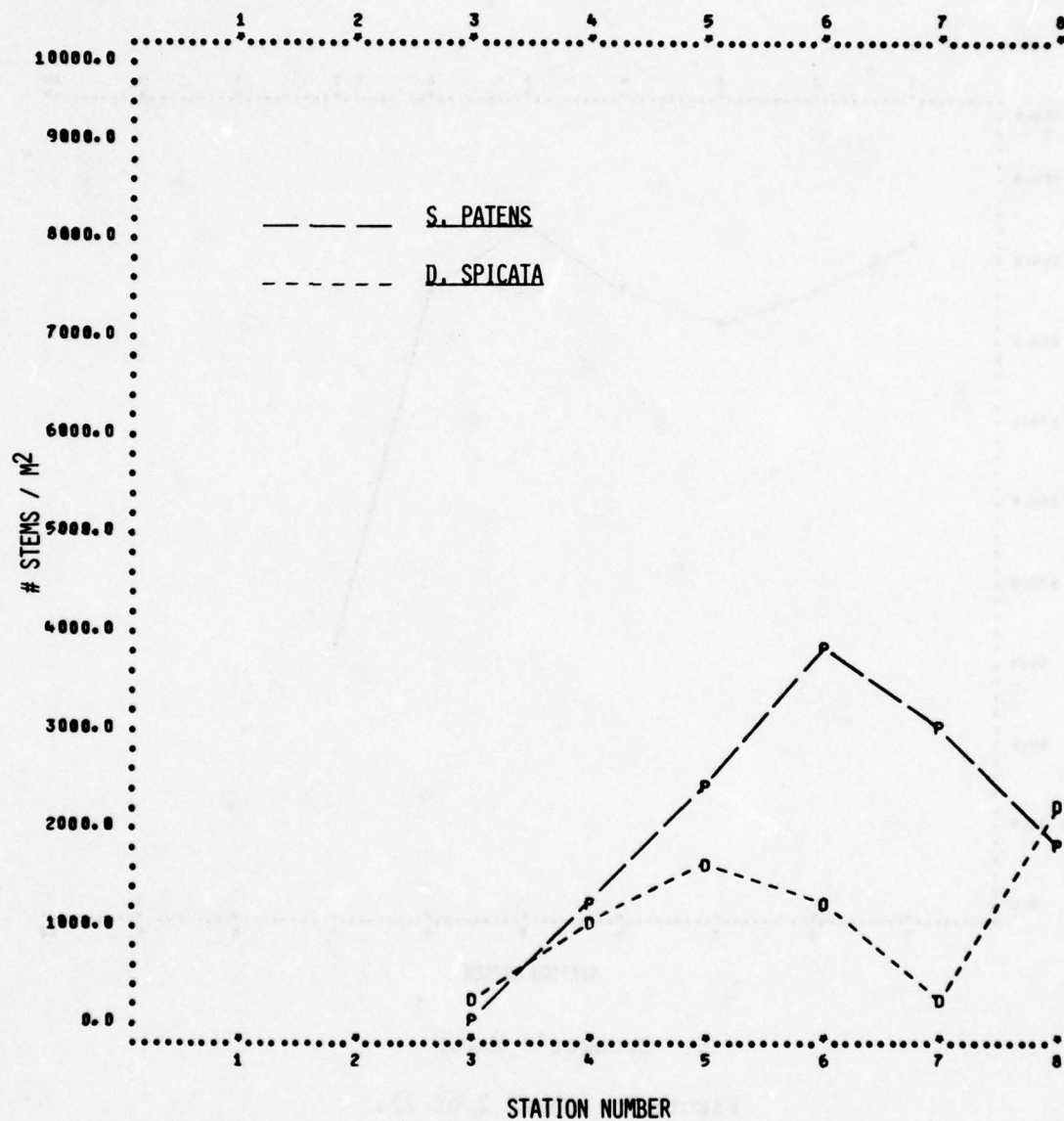
a. Taskinas Marsh

Figure 8. Maximum values for stem density of Spartina patens and Distichlis spicata at Taskinas Marsh and Bennett's Marsh (sheet 1 of 2).
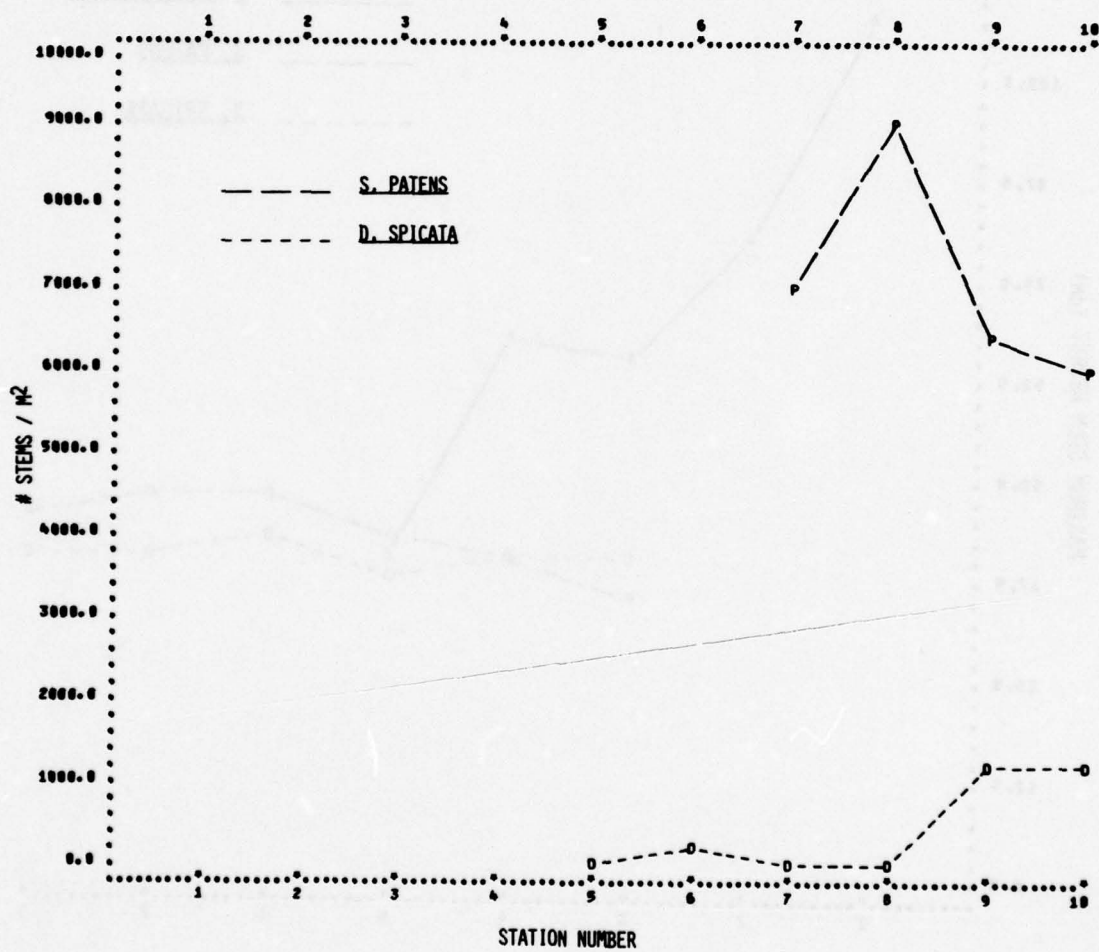
b. Bennett's Marsh

Figure 8 (sheet 2 of 2).

MAXIMUM STEM HEIGHT (CM)

125.0

112.5

100.0

87.5

75.0

62.5

50.0

37.5

25.0

12.5

0.0

1   2   3   4   5   6   7   8

	S. ALTERNIFLORA
	S. PATENS
	D. SPICATA

STATION NUMBER
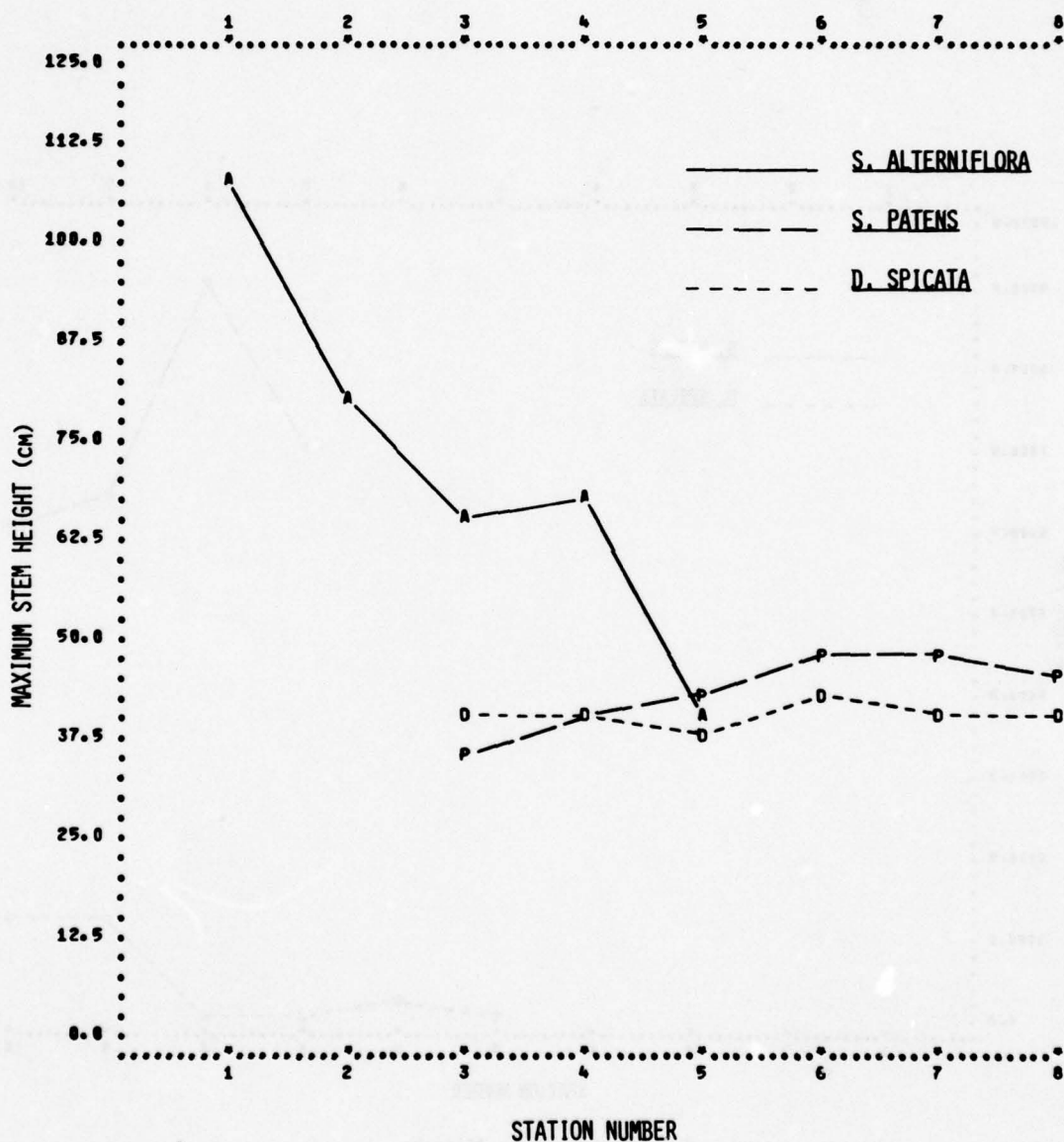
a. Taskinas Marsh

Figure 9. Maximum values for stem height of Spartina patens and Dis-
tichlis spicata at Taskinas Marsh and Bennett's Marsh
(sheet 1 of 2).

44
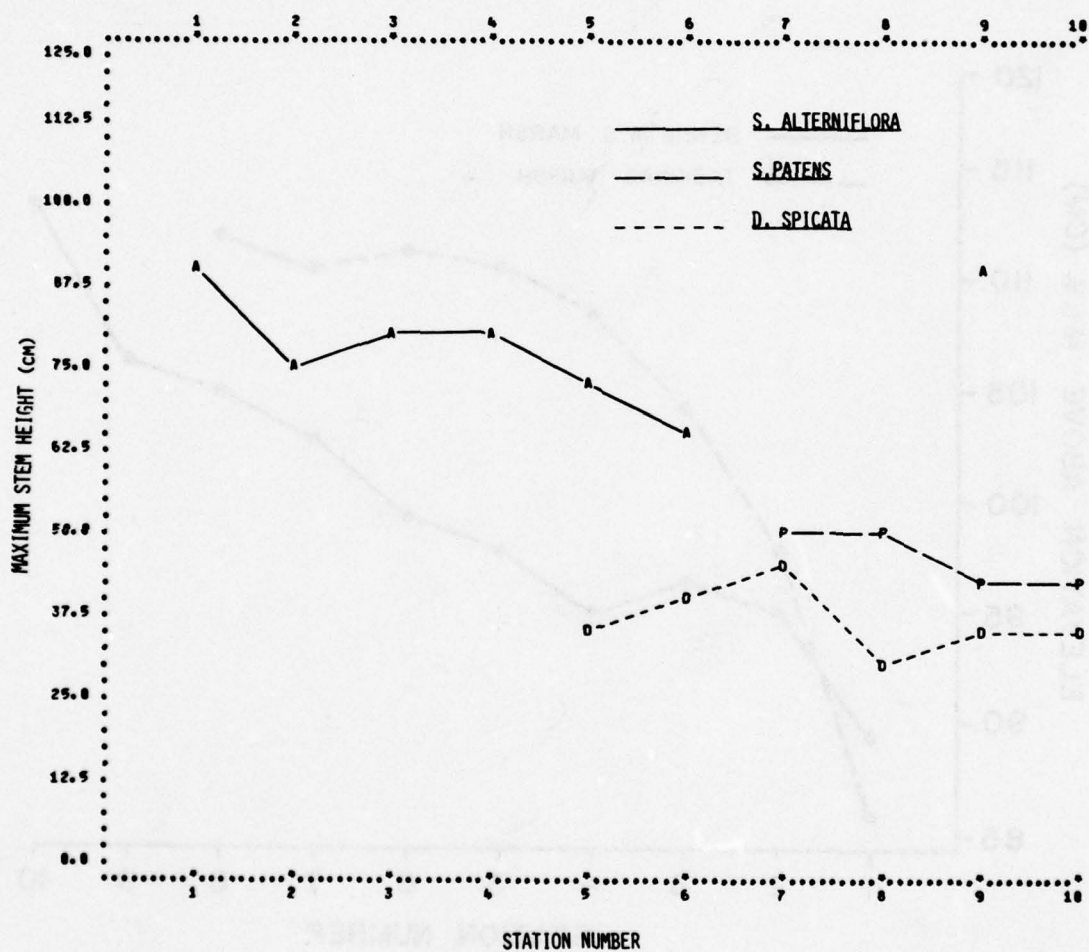
b. Bennett's Marsh

Figure 9 (sheet 2 of 2).

45
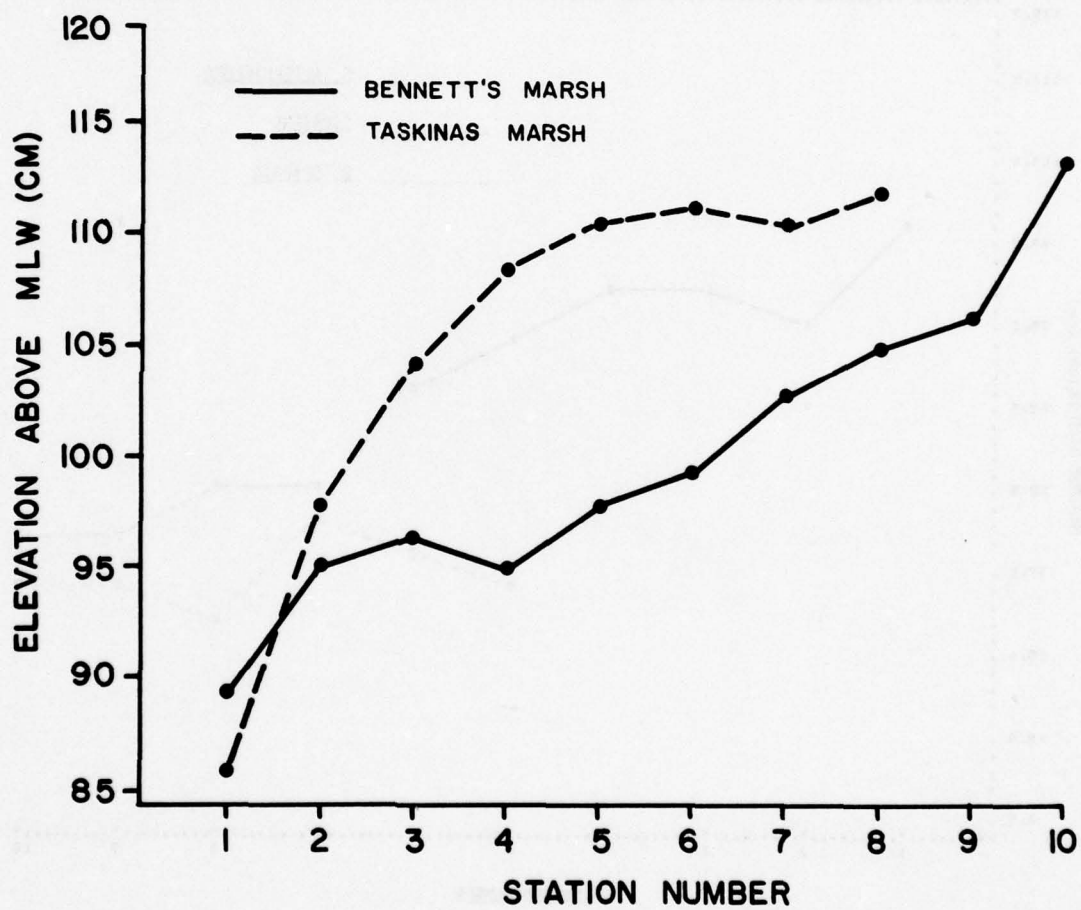
Figure 10.   Elevation of the sample stations above mean low water.

46

a) Elevation at Taskinas Marsh increased sharply rearward from the low marsh (zones 1-4), then leveled off in the high marsh (zones 5-8). Bennett's Marsh also rose toward the rear, but with a more gradual, constant slope than Taskinas Marsh.

b) The slightly mounded profile of Bennett's low marsh, centered on zone 3, was a natural levee. Levees are common features of sloping marsh foreshores (Kurz and Wagner, 1957). No such structure existed in the Taskinas low marsh.

c) Most of the Taskinas site was considerably higher above mean low water than the Bennett's Creek site.

Number of inundations

49. A FORTRAN computer program (Program TIDE) translated elevation data into estimates of the number of inundation events per year at each sample zone. An inundation event was defined as any instance in which tidal water covered the sediment surface. The results can be summarized as follows (Figure 11):

a) The sharpest deline in number of inundations occurred between zones 1 and 2 (the zones closest to the tidal creek) in each marsh.

b) Inundation events declined rapidly away from the creek at Taskinas low marsh; in fact, no inundation at all is predicted landward of zone 3. At Bennett's Marsh, inundation dropped more gradually toward the rear, and only the two highest zones (9 and 10) were above the reach of predicted tides.

50. Thus, predicted tidal inundation was considerably more

47
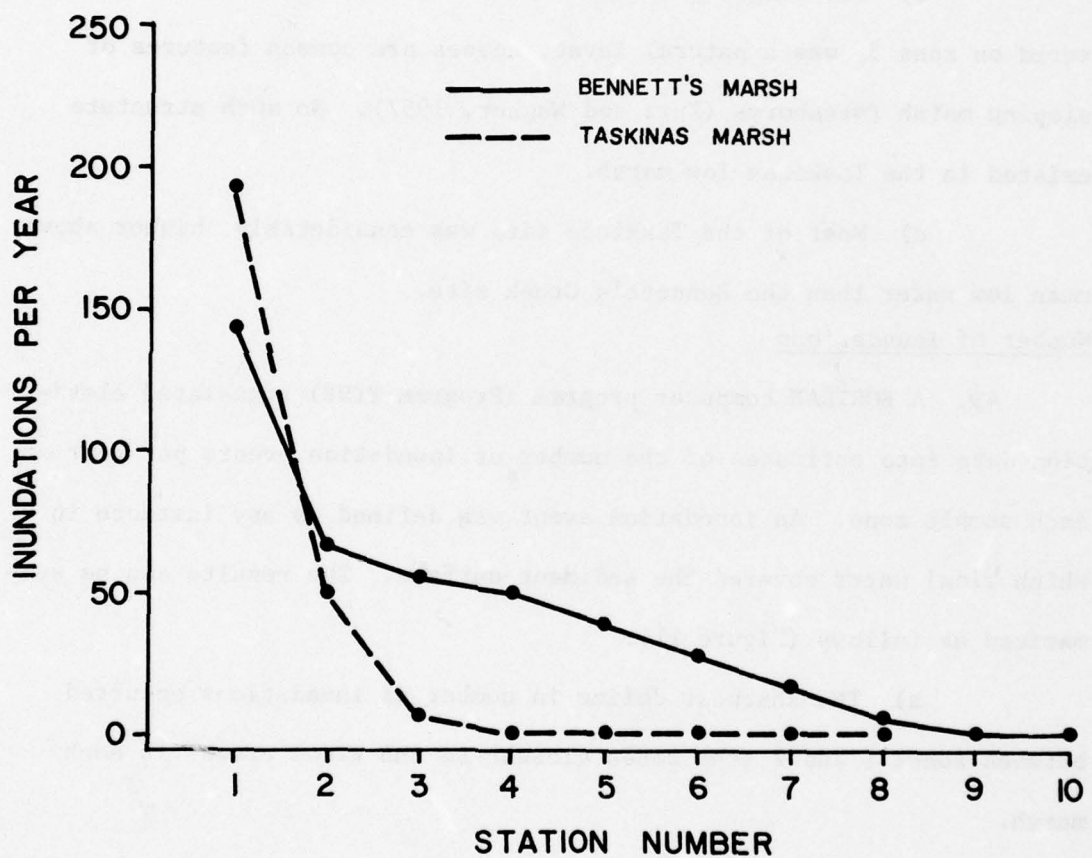
Figure 11. Number of inundations per year at sample stations.

extensive at Bennett's Marsh than at Taskinas Marsh. As previously
stated, the fact that L/D ratios (living:dead standing crop) at
Bennett's exceeded those at Taskinas in both low marsh and high marsh
corroborates the prediction of greater flooding at the Bennett's Creek
site (Mendelssohn, 1973).

Salinity

51. Interstitial salinity (Figure 12) increased relatively
sharply across the low marsh at Taskinas (zones 1-4), then peaked in the
ecotone (zones 4-5) and declined in the high marsh. Salinity at Bennett's
Marsh rose initially to a small peak at zone 2, then declined slightly
before increasing again in the high marsh.

52. Although they are not shown by the averaged values in Figure
12, maximum soil salinities exceeded 20 o/oo at both sites, a concentra-
tion exceeding the highest values measured in the creek water (about
15 o/oo). Soil salinities exceeding the maximum salinity of tidal water
have also been noted in other brackish estuarine marshes (Lindberg and
Harriss, 1973).

Organic matter

53. Samples from both marshes showed a nearly linear increase in
percent organic matter from the low marsh through the high marsh (Figure
13). Taskinas Marsh had the greater range, possessing both the lowest
value (zone 1) and the highest value (zone 8). The rearward increase in
organic matter at Bennett's Marsh was more gradual and somwehat less
linear than at Taskinas Marsh. Buttery et al. (1965) noted a similar
rise in organic matter content from low marsh to high marsh.

54. The organic content of tidal marsh sediments is largely a

49
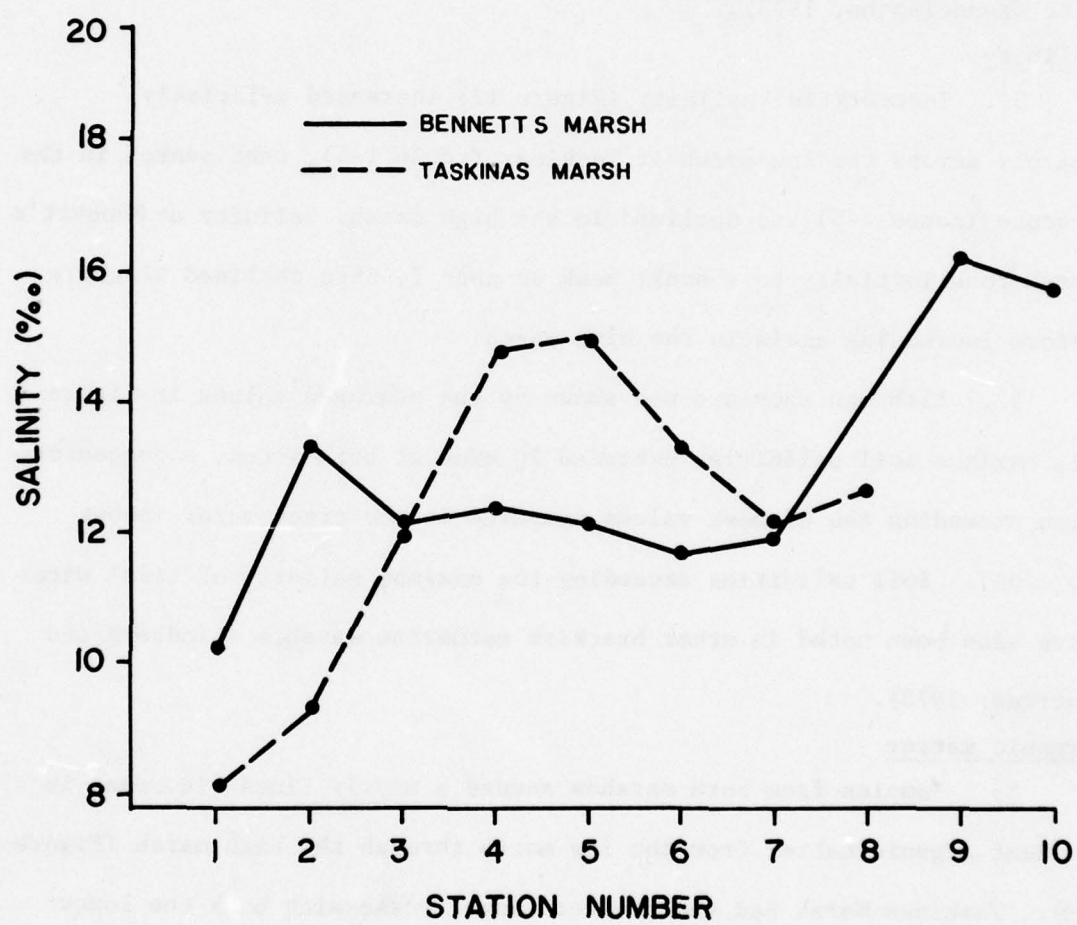
Figure 12. Salinity of interstitial water.

50
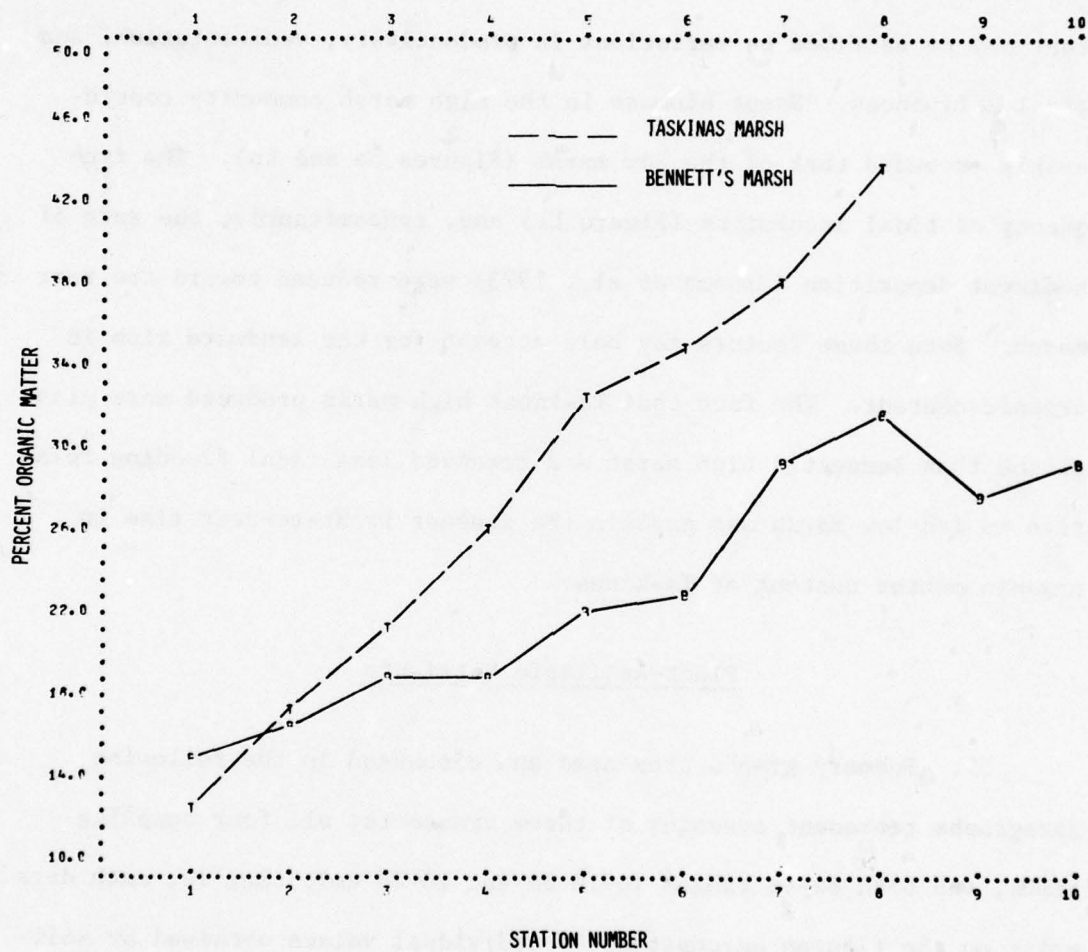
Figure 13. Percent organic matter of marsh sediments.

function of the amount of plant material produced in situ, together with the effects of consumption, decay, sedimentation, and tidal flushing. Assuming that consumption and decay rates were roughly comparable at Taskinas Marsh and Bennett's Marsh, the differences in organic content may be ascribed to variations in productivity, sedimentation, and tidal influences. Shoot biomass in the high marsh community considerably exceeded that of the low marsh (Figures 5a and 5b). The frequency of tidal incursions (Figure 11) and, concomitantly, the rate of sediment deposition (Broome et al., 1973) were reduced toward the rear marsh. Both these factors may help account for the landward rise in organic content. The fact that Taskinas high marsh produced more plant tissue than Bennett's high marsh and received less tidal flooding relative to its low marsh may explain the steeper front-to-rear rise in organic matter content at Taskinas.

Plant-Available Nutrients

55. Summary graphs presented and discussed in the following paragraphs represent averages of three transects, all four sampling times, and both depth ranges (0-10 cm and 10-20 cm); that is, each data point on the figures encompasses 24 individual values obtained by sediment analysis. The means and standard errors for the habitat variables are given in Table 1.

Ammonia-N

56. Summary values for estimated plant-available ammonia-N (Figure 14) indicated that, at both marshes, slightly higher values tended to characterize the high marsh sediments. However, the range of

52

Table 1

Means (X̄) and Standard Errors (S.E.M.) of Habitat Parameters from the Study Sites

Sample Zone	Elevation (n=3)		Inundation (n=3)		Organic Matter (n=6)		Salinity (n=3)		NH₃-N (n=24)		PO₄-P (n=24)		Ca (n=24)		Mg (n=24)		Mn (n=24)		Fe (n=24)	
	X̄ (cm)	S.E.M.	X̄ (#/yr)	S.E.M.	X̄ (%)	S.E.M.	X̄ (%)	S.E.M.	X̄ (ppm)	S.E.M.	X̄ (ppm)	S.E.M.	X̄ (ppm)	S.E.M.	X̄ (ppm)	S.E.M.	X̄ (ppm)	S.E.M.	X̄ (ppm)	S.E.M.
Taskinas Marsh																				
1	86.0	2.1	192.7	38.5	13.1	0.2	8.0	--	7.5	1.0	16.1	4.6	406.5	17.7	677.5	27.4	94.0	11.3	1104.8	80.0
2	97.7	--	52.0	34.2	17.3	0.6	9.3	6.6	7.2	1.1	62.5	8.9	426.5	13.0	762.3	22.3	33.7	3.9	797.5	69.7
3	104.3	2.2	7.7	5.7	21.6	1.3	12.0	--	6.4	0.9	82.5	8.0	470.3	17.9	887.8	33.3	18.8	2.1	634.6	67.8
4	108.3	1.2	1.7	0.7	26.5	1.4	14.8	1.8	8.1	1.3	85.0	9.4	467.0	18.6	894.7	43.9	15.5	2.9	722.3	93.3
5	110.3	0.3	0.0	--	32.7	2.1	15.0	1.0	6.9	1.1	95.3	7.4	449.6	19.5	829.6	49.7	13.9	2.6	665.2	99.2
6	111.0	0.3	0.0	--	34.9	0.8	13.4	1.2	6.8	0.9	117.3	9.0	438.8	17.0	815.8	45.0	6.7	1.1	590.7	104.9
7	110.7	1.2	0.0	--	38.4	1.8	12.1	1.1	8.5	1.5	104.7	5.6	430.4	16.0	775.0	34.2	5.7	1.2	319.9	53.6
8	112.0	0.6	0.0	--	43.6	1.8	12.8	0.7	8.1	1.1	105.1	7.2	439.1	16.0	749.8	27.9	5.0	1.0	374.0	62.2
Bennett's Marsh																				
1	89.3	0.9	147.3	14.2	15.1	0.4	10.4	--	6.0	0.7	105.7	11.7	422.0	28.7	731.3	29.1	12.7	1.0	600.8	46.1
2	95.3	0.3	69.7	3.3	16.9	0.7	13.3	--	6.9	1.2	151.7	7.8	433.6	28.4	802.1	32.3	5.6	0.5	532.7	46.0
3	96.3	0.7	58.8	7.3	18.9	0.6	12.1	0.7	6.6	0.8	155.0	4.7	428.3	10.7	850.0	23.5	4.4	0.4	477.0	40.5
4	95.0	1.0	54.3	8.7	19.2	0.4	12.5	0.7	8.1	1.0	154.6	4.9	444.2	9.9	896.6	16.4	3.6	0.2	351.6	26.3
5	98.0	0.6	41.3	5.2	22.5	1.1	12.3	0.6	7.7	0.9	140.6	3.9	419.1	11.4	829.1	25.3	3.2	0.3	339.0	28.8
6	99.7	0.9	30.7	5.0	23.3	0.6	11.6	--	7.8	0.8	129.9	3.2	383.0	6.7	754.9	21.3	2.3	0.2	291.6	41.3
7	103.0	0.6	17.0	1.7	29.7	2.1	11.9	0.9	8.5	0.8	133.4	4.5	360.6	14.2	729.8	43.9	3.9	0.6	259.8	41.9
8	105.0	0.6	10.0	2.3	31.7	2.3	14.0	1.9	6.8	1.1	144.8	7.2	388.7	12.2	786.9	38.1	2.7	0.3	215.9	40.0
9	106.7	0.3	4.0	1.0	28.0	2.0	16.2	1.4	8.7	1.2	136.7	13.0	499.6	10.9	991.8	34.4	3.3	0.3	963.2	83.6
10	113.3	2.2	1.3	0.3	29.5	2.5	15.7	1.7	8.5	1.7	113.5	15.4	500.6	14.1	981.6	42.2	5.5	0.9	1045.2	96.4

Note: Nutrient data include 4 sampling periods (4-5 April, 29-30 May, 21 July, and 13 September) and 2 depth ranges in sediment (0-10 cm and 10-20 cm). Sample zones are numbered consecutively along transects from low marsh to high marsh; transect length = 28 m (Taskinas Marsh) and 36 m (Bennett's Marsh).

NH₃ - N (PPM)

STATION NUMBER

TASKINAS MARSH
BENNETT'S MARSH
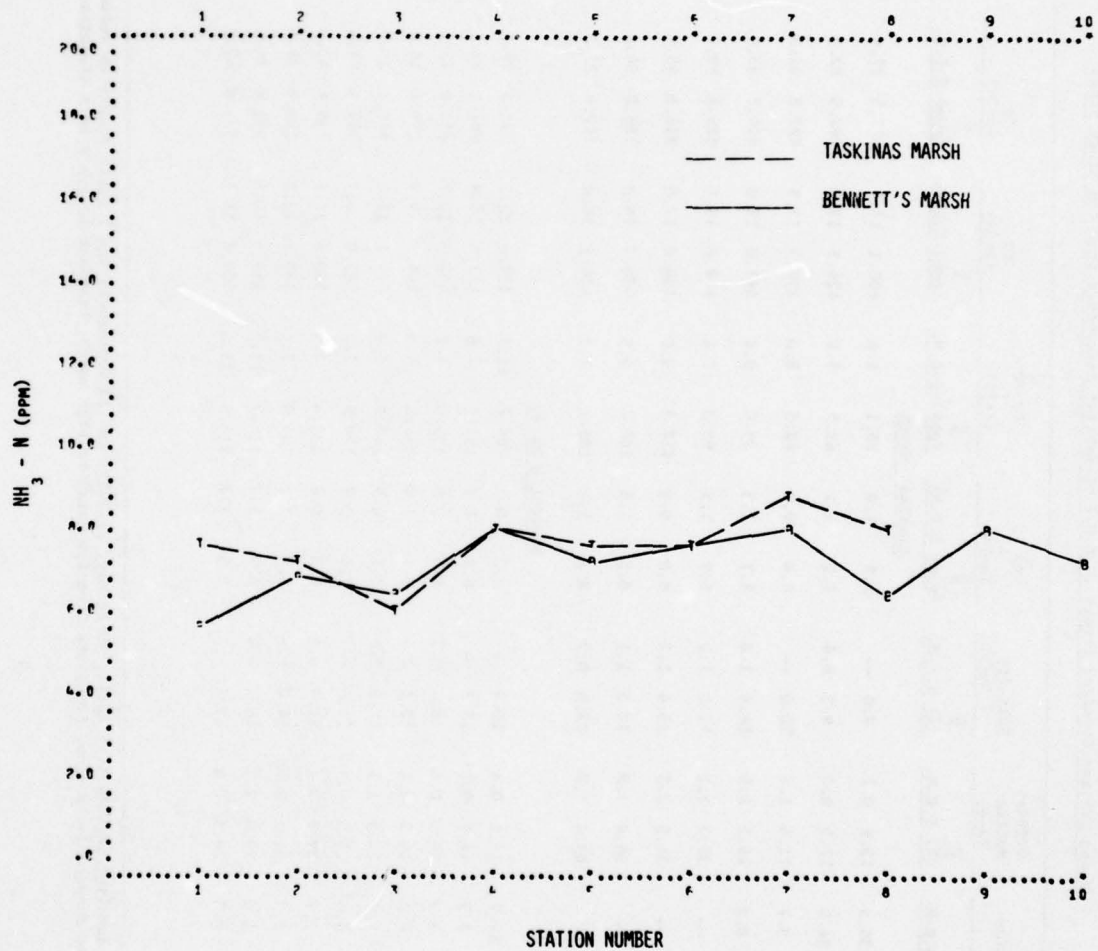
Figure 14. Concentration (ppm) of plant-available ammonia-N in
marsh sediments at sample stations.

54

variation was small (5.5-9.0 ppm) and clear patterns of spatial change were not evident.

57. Jeffrey (in Piggott, 1969) also found that concentrations of ammonia exhibited little pattern across a marsh. However, since inorganic nitrogen can change quite rapidly in form and amount in soils (by microbial uptake and release, plant absorption, volatilization, immobilization in humus, absorption within crystal lattices, and mineralization of organic matter) concentrations of ammonia-N at a few instants of time may not accurately represent the soil's capacity to supply inorganic nitrogen to plants over an entire growing season (Tusneem and Patrick, 1971).

Phosphate

58. Both marshes displayed a relatively rapid increase in available phosphate concentration from zone 1 to zone 2 (Figure 15). Piggott (1969) also reported a landward increase in phosphorus content of marsh soils. At Taskinas, the values continued to increase rearward but at a slower rate, leveling off in the high marsh. The Bennett's Creek transect showed two small peaks, one each in the high marsh and low marsh, with a slight trough toward the rear of the ecotone(zone 6). Concentrations at Taskinas were generally somewhat lower than at Bennett's Creek.

Iron

59. Concentrations of plant-available iron declined gradually from the low marsh toward the rear zones at both study sites (Figure 16). At Taskinas, the concentrations were somewhat higher and the rearward decline was less linear than at Bennett's. However, zones 9 and 10 mark a major departure: a sudden steep increase in concentration,

$PO_4 - P$ (PPM)

200.0
180.0
160.0
140.0
120.0
100.0
80.0
60.0
40.0
20.0
0.0

1 2 3 4 5 6 7 8 9 10

STATION NUMBER
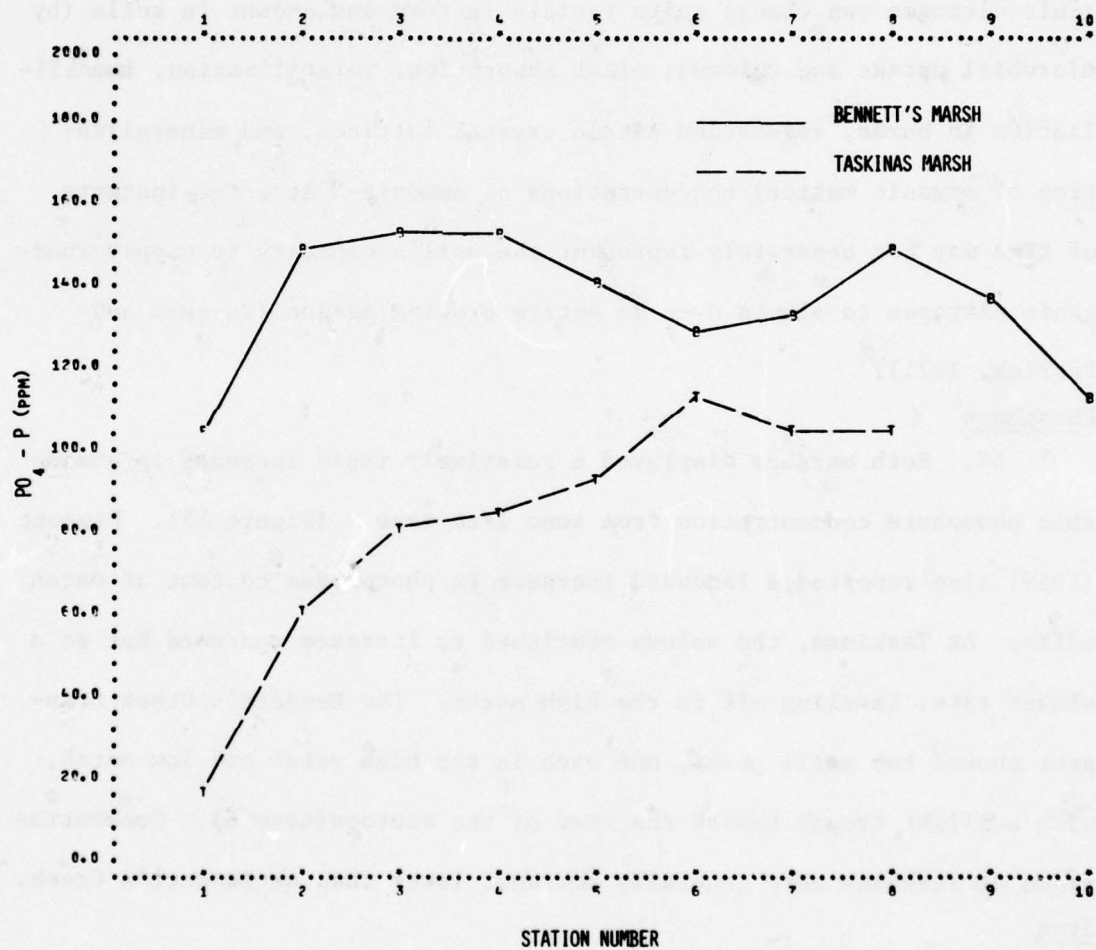
Figure 15. Concentrations (ppm) of plant-available phosphate-P in
marsh sediments at sample stations.

IRON (PPM)

1500.0

1350.0

1200.0 ·· – – – – TASKINAS MARSH

BENNETT'S MARSH

1050.0

900.0

750.0

600.0

450.0

300.0

150.0

0.0

1 2 3 4 5 6 7 8 9 10

STATION NUMBER
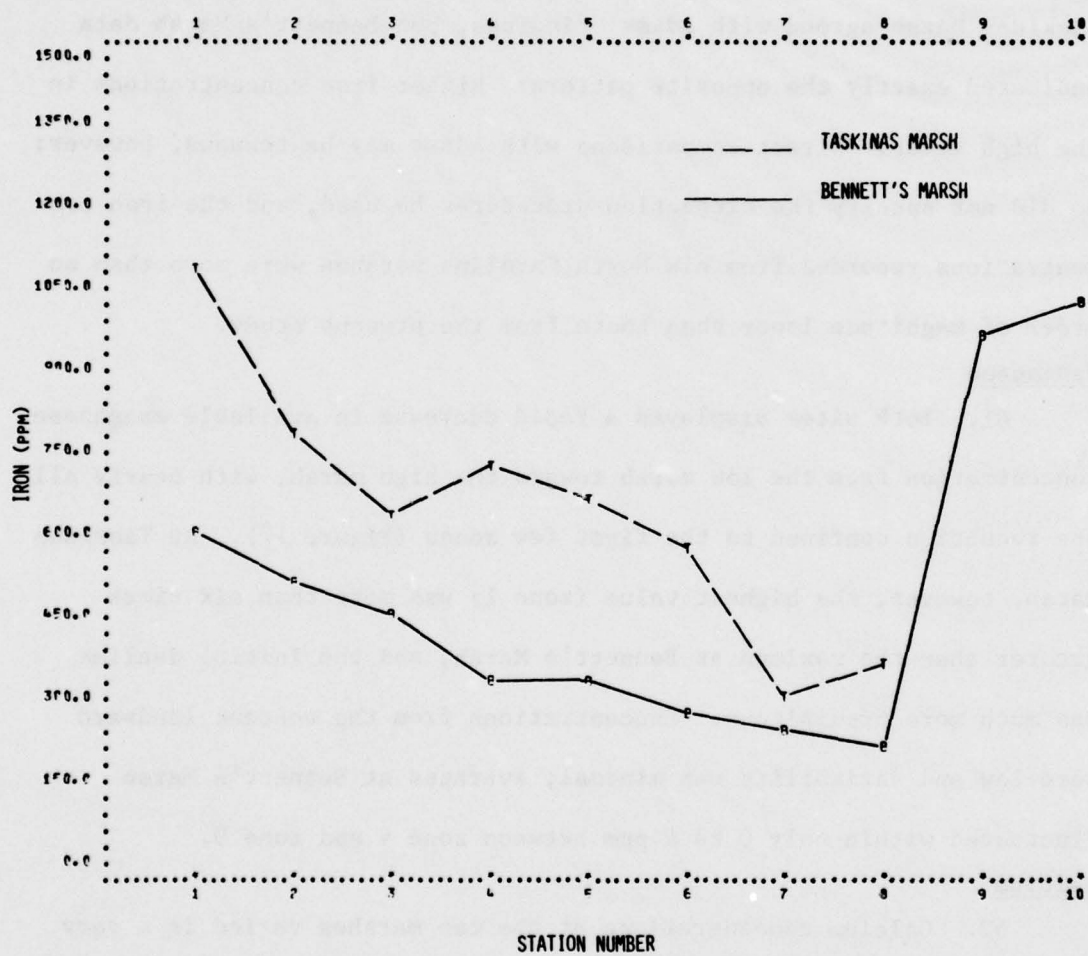
Figure 16. Concentration (ppm) of plant-available iron in marsh
sediments at sample stations.

attaining the highest values recorded for Bennett's Marsh.

60. The results varied with regard to Adams' (1963) contention that tall S. alterniflora tended to be associated with higher iron concentrations than the S. patens - D. spicata association. The data from Taskinas Marsh agreed with Adams' findings, but Bennett's Marsh data indicated exactly the opposite pattern: higher iron concentrations in the high marsh. Direct comparisons with Adams may be tenuous, however; he did not specify the extraction procedures he used, and the iron concentrations recorded from his North Carolina marshes were more than an order of magnitude lower than those from the present study.

Manganese

61. Both sites displayed a rapid decrease in available manganese concentration from the low marsh toward the high marsh, with nearly all the reduction confined to the first few zones (Figure 17). At Taskinas Marsh, however, the highest value (zone 1) was more than six times greater than the maximum at Bennett's Marsh, and the initial decline was much more precipitous. Concentrations from the ecotone landward were low and variability was minimal; averages at Bennett's Marsh fluctuated within only 0 to 4 ppm between zone 4 and zone 9.

Calcium

62. Calcium concentrations at the two marshes varied in a very similar manner (Figure 18). Both exhibited a peak value in the low marsh adjacent to the ecotone, a decline rearward through the ecotone, and some upward recovery in the high marsh (the latter trend was more evident at Bennett's Creek Marsh).
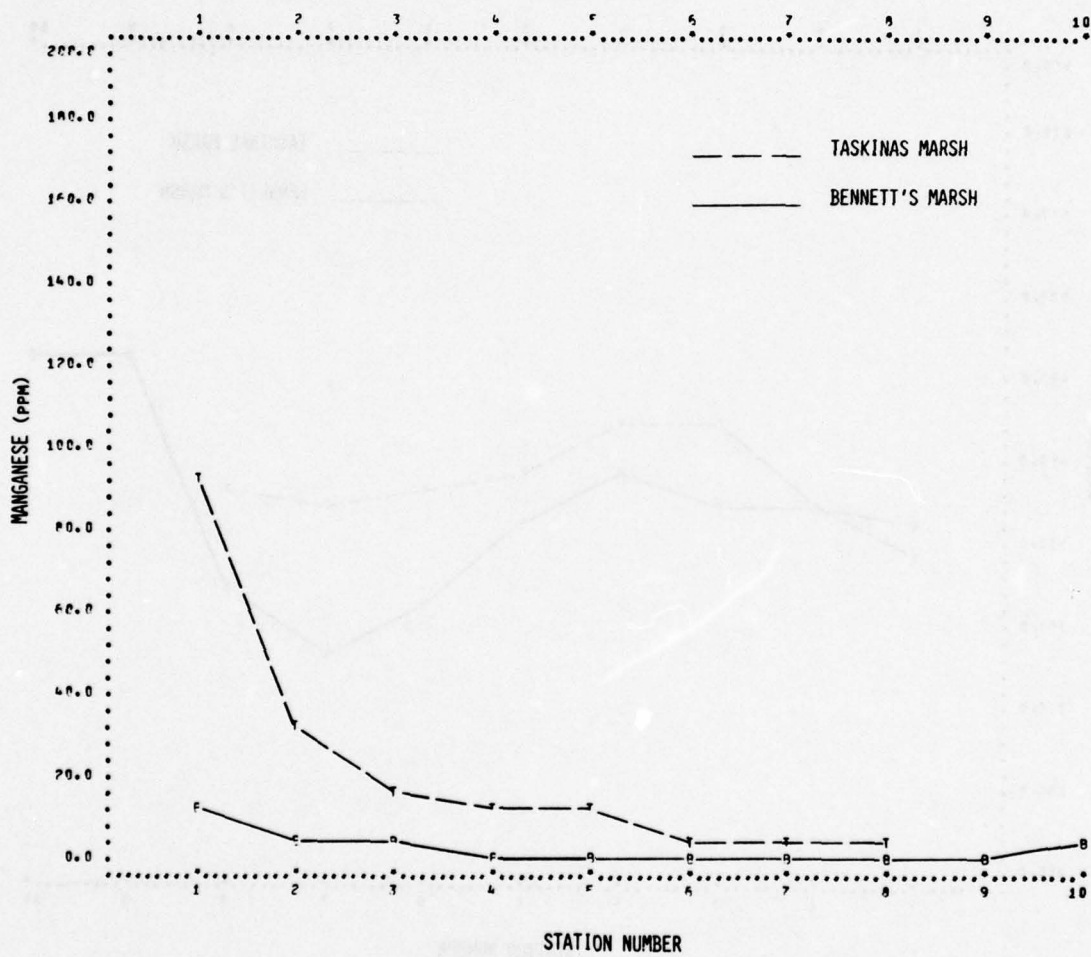
Figure 17. Concentration (ppm) of plant-available manganese in
marsh sediments at sample stations.

59
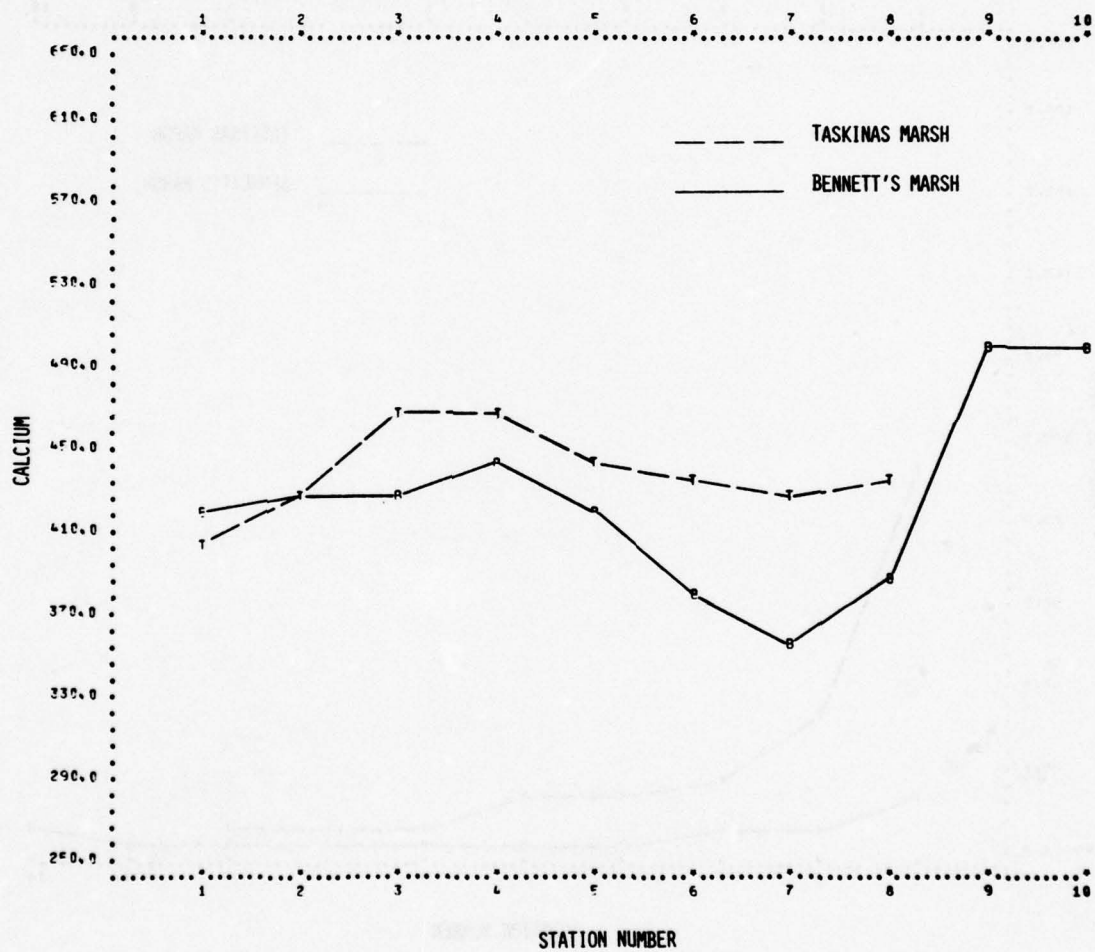
Figure 18. Concentration (ppm) of plant-available calcium in
marsh sediments at sample stations.

60

Magnesium

63. The graphs of available magnesium (Figure 19) showed a striking resemblance to the pattern for calcium (Figure 18). As with calcium, both marshes varied in nearly identical fashion: high values occurred at the seaward edge of the ecotone, and Bennett's Marsh attained its highest concentrations in zones 9 and 10.

Correlation Analyses

64. Statistical correlation is a useful first step toward identifying the habitat factors most closely related to plant growth and distribution. Bivariate correlation is a statistical technique for measuring the intensity of relationship between co-occurring variables. The correlation statistic employed here is the Pearson product-moment correlation coefficient, "r".

65. The test used assumes that the data are randomly sampled, normally distributed, and there is a linear relation between the variables. The data set was sufficient to generally satisfy the latter two correlations. The data were sampled by a form of stratified random method, whereby samples were collected randomly from within specified sample areas. Values of "r" and their associated statistical significance were calculated with the "Scattergram" subprogram of _Statistical Package for the Social Sciences_ (SPSS) (Nie et al., 1975).

66. Tables 2 and 3 display correlation coefficients relating plant growth variables to habitat variables at Taskinas Marsh and Bennett's Marsh, respectively. The three growth variables measured--

61
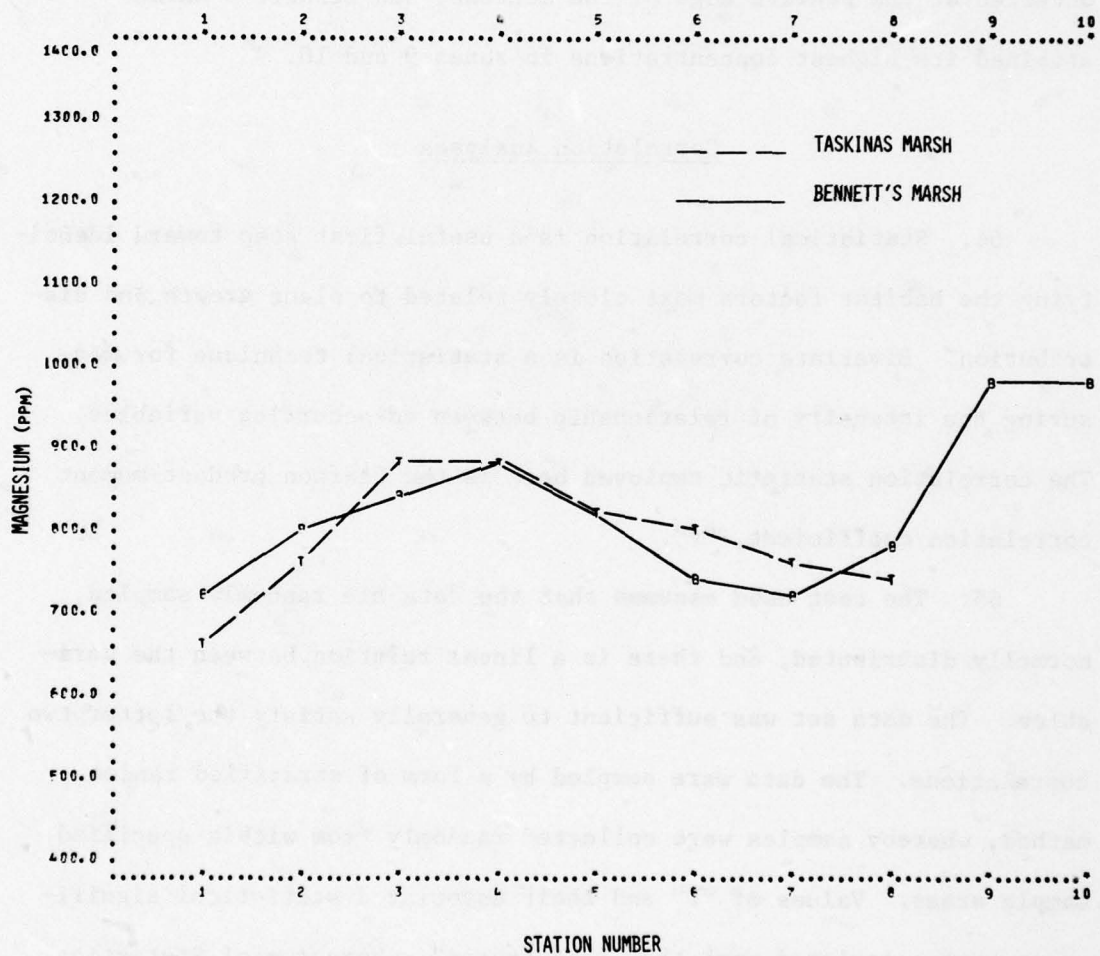
Figure 19.   Concentration (ppm) of plant-available magnesium in
marsh sediments at sample stations.

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Table 2

Correlation Coefficients Between Plant Variables and Habitat

Variables at Taskinas Marsh

Species	Plant Variable	Elevation cm*	No. of inundations per year	Organic Matter %	Salinity ppm	NH$_3$ ppm	PO$_4$ ppm	Ca ppm	Mg ppm	Mn ppm	Fe ppm
					Habitat Variable						
S. alterniflora	Standing Crop	-0.76**	0.73**	-0.82**	-0.50	-0.46	-0.73**	-0.22	-0.38	0.77**	0.61
(df = 22)	Stem Height	-0.85**	0.84**	-0.67*	-0.79**	0.05	-0.52	-0.75**	-0.88**	0.72**	0.31
	Stem Density	0.35	-0.28	0.07	0.68	-0.18	-0.07	0.41	0.53	-0.09	0.12
S. patens	Standing Crop	0.53*	-0.36	0.32	0.27	-0.05	0.04	-0.14	0.02	-0.19	0.21
(df = 34)	Stem Height	0.26	0.04	0.18	-0.46	0.45	-0.40	-0.01	-0.21	-0.31	-0.21
	Stem Density	0.39	-0.07	0.05	0.30	-0.49	-0.18	-0.22	-0.02	-0.08	-0.12
D. spicata	Standing Crop	0.45	0.22	0.57*	-0.16	0.34	0.47	-0.18	-0.50*	-0.47*	-0.33
(df = 34)	Stem Height	0.12	0.43	0.14	-0.47	0.11	0.33	0.14	-0.31	-0.35	-0.11
	Stem Density	0.41	-0.13	-.49	-0.02	0.19	0.41	-0.26	-0.44	-0.37	-0.33

NOTE: Standing crop represents maximum live standing crop; stem height and density are average values of July and September data.

* Significant at 5% level

** Significant at 1% level

Table 3

Correlation Coefficients Between Plant Variables and Habitat Variables at Bennett's Marsh

Species	Plant Variable	Elevation cm	No. of Inundations per year	Organic Matter %	Salinity ppm	NH_3 ppm	PO_4 ppm	Ca ppm	Mg ppm	Mn ppm	Fe ppm
S. alterniflora	Standing Crop	-0.73**	0.58**	0.77**	-0.55**	-0.06	-0.10	0.54*	0.19	0.44*	0.54*
(df = 40)	Stem Height	-0.80**	0.69**	0.71**	-0.38	0.20	-0.30	0.34	-0.03	0.66**	0.49
	Stem Density	-0.04	0.05	-0.15	-0.31	-0.31	-0.25	0.03	-0.14	0.01	-0.09
S. patens	Standing Crop	-0.44	0.72**	0.14	-0.56	0.25	0.22	-0.83**	-0.79**	-0.12	-0.71**
(df = 34)	Stem Height	-0.40	0.53	0.14	-0.17	0.30	0.37	-0.55	-0.57	-0.21	-0.65*
	Stem Density	0.39	-0.32	0.63*	0.27	-0.53	0.34	0.17	-0.16	-0.38	-0.05
D. spicata	Standing Crop	0.68**	-0.65**	0.27	0.59**	-0.07	-0.12	0.71**	0.62**	0.15	0.76**
(df = 34)	Stem Height	-0.17	-0.05	0.34	-0.11	0.15	0.11	-0.43	-0.25	-0.25	-0.26
	Stem Density	0.81**	-0.75**	0.31	0.79**	-0.14	-0.04	0.75**	0.70**	0.21	0.79**

(Habitat Variable)

NOTE: Standing crop represents maximum live standing crop; stem height and density are average values of July and September data.

* Significant at 5% level
** Significant at 1% level

standing crop, stem height, and stem density--are listed for each of the three predominant plant species: S. alterniflora, S. patens, and D. spicata.

67. Several of the plant-habitat correlations deserved special emphasis. It was evident from comparing spatial patterns of standing crop (Figure 5) and stem height (Figure 8) with elevation and inundation (Figures 10 and 11) that growth of S. alterniflora exhibited a highly significant positive correlation with tide factors. This relationship had been observed repeatedly (Johnson and York, 1915; Adams, 1963; Kurz and Wagner, 1957); but since the sampling sites in the present study did not extend to the seaward extreme of S. alterniflora distribution, the contention that tidal inundation restricted the species along the lower margin of its range within the marsh (Johnson and York, 1915; Teal and Kanwisher, 1961) could not be tested. For S. patens and D. spicata, the measured responses to tides differed conspicuously between the two marshes. At Taskinas, where tidal water very seldom reached the high marsh (Figure 10) growth of neither species was closely related to inundation or elevation; Bennett's high marsh, which received some regular flooding during spring tides, showed close correlations of tide with S. patens (positive) and D. spicata (negative).

68. As indicated by previous investigators (Gosselink, 1970; Palmisano, 1970; Phleger, 1971), growth of certain species tends to be inhibited by increasing soil salinity. Negative correlations were significant for S. alterniflora at both marshes and less pronounced for S. patens. D. spicata, the most salt-tolerant of the three species

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(Adams, 1963), showed positive correlations with salinity at Bennett's Marsh.

69. The absence of significant correlations between ammonia-N concentration and growth of any species appears to support Tusneem and Patrick's (1971) contention that sampling only at isolated instances (as was done in this study) may misrepresent the plant response to soil nitrogen over a growing season. The fact that nitrogen availability clearly limits growth of marsh grasses (Valiela and Teal, 1973; D.E. Marshall, 1970; Broome et al., 1973), coupled with the low concentrations found in the soil (Figure 14). suggested that rapid depletion by plant uptake may engender considerable fluctuation of ammonia-N levels. Analysis of available nitrogen in both soil and plant tissue at frequent intervals over the growing season might provide a better measure of plant response to soil nitrogen. Working with aquatic species, Gerloff and Krombholz (1966) noted a critical level of nitrogen concentration in plant tissues of 1.3 percent below which growth was inhibited; similar data for salt marsh species would help elucidate the relationship between plant growth and nitrogen availability in soils.

70. Phosphate concentrations were not closely correlated with plant growth, either. Since fine-textured, highly reduced sediments, such as typify Taskinas Marsh and Bennett's Marsh, usually possess abundant available phosphorus (Broome et al., 1973), the absence of a close relationship with plant growth was not surprising.

71. S. alterniflora standing crop correlated significantly with iron availability at both marshes, supporting the theory that this

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species thrives where iron is plentiful (Adams, 1963; Mooring et al., 1971; Nixon and Oviatt, 1973). S. patens and D. spicata showed opposite patterns of correlation at Bennett's Marsh: S. patens was negatively correlated to iron, while D. spicata had a highly significant positive correlation.

72. A contrast is discernible between Table 2 and Table 3 in the arrangement of significant correlations. Significant plant-habitat correlations were almost entirely restricted to S. alterniflora at Taskinas Marsh, while all three species exhibited significant correlations at Bennett's Marsh. This difference suggests that more of the habitat factors measured were closely related to growth of high marsh species (S. patens and D. spicata) at Bennett's Marsh than at Taskinas Marsh.

73. Figure 10 and Figure 11 indicate that while Taskinas Marsh received no regular tidal influence, Bennett's high marsh was inundated to some extent. This pattern of correlations appeared to support the hypothesis (Hinde, 1954; Gray and Bunce, 1972) that tidal changes in water level may exert a controlling influence upon plant growth by modification of other habitat conditions.

74. Tables 4 and 5 are matrices of correlation coefficients that indicate the intensity of relationships among habitat factors. Values of "r" and their significance were calculated for the distinct communities in each marsh. Low marsh correlations included only the range of S. alterniflora, while high marsh correlations were restricted to the S. patens - D. spicata community.

Table 4

Correlation Coefficients between Habitat Variables at Taskinas Marsh

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
(1) Elevation	--	--	0.23	0.64**	-0.12	0.08	-0.21	-0.25	-0.29	-0.03
(2) # of Inundations	--	--	-0.23	-0.30	-0.23	0.12	0.11	0.18	-0.04	-0.18
(3) Salinity	0.87*	-0.70	--	-0.43	-0.64*	-0.71**	0.33	0.63**	0.70**	0.61*
(4) Organic Matter	0.77**	-0.72**	0.67	--	0.34	0.57*	-0.53*	-0.69**	-0.81**	0.59**
(5) Ammonia-N	0.67*	-0.03	0.98*	0.23	--	0.55	-0.47	-0.38	-0.32	-0.53
(6) Phosphate-P	0.58	-0.62*	0.20	0.84**	-0.03	--	-0.53*	-0.80**	-0.88**	-0.80**
(7) Calcium	0.67*	-0.65*	0.69	0.52	-0.21	0.27	--	0.73**	0.58	0.82*
(8) Magnesium	0.71	-0.65*	0.84*	0.57*	-0.02	0.32	0.91*	--	0.79**	0.84**
(9) Manganese	-0.79**	0.87**	-0.52	-0.78**	0.18	-0.82**	-0.63**	-0.59*	--	0.60*
(10) Iron	0.37	0.41	-0.04	-0.68**	-0.10	0.92**	0.00	-0.11	0.53*	--

* = significant at 5% level; ** = significant at 1% level.
Note: Values above the main diagonal are for the high marsh; values below the main diagonal are for the low marsh.

Table 5

Correlation Coefficients between Habitat Variables at Bennett's Marsh

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
(1) Elevation	--	--	0.43	0.42	0.65**	-0.10	0.59**	0.58*	0.50*	0.65**
(2) # of Inundations	--	--	-0.52**	-0.61**	0.45	0.03	-0.49**	-0.58*	-0.27	-0.65**
(3) Salinity	-0.05	-0.28	--	0.11	0.38	-0.25	0.65*	0.49	0.47	0.69**
(4) Organic Matter	0.83**	-0.73**	0.18	--	0.29	0.18	0.04	0.08	-0.15	0.02
(5) Ammonia-N	-0.79**	-0.23	0.78**	0.38	--	-0.01	0.08	-0.05	0.46	0.16
(6) Phosphate-P	0.26	-0.45**	0.57*	-0.02	0.11	--	-0.12	-0.05	-0.71**	0.65*
(7) Calcium	-0.50	0.40	-0.16	-0.60**	0.24	0.14	--	0.96**	0.32	0.84**
(8) Magnesium	0.04	-0.23	0.14	-0.18	-0.11	0.72**	0.61**	--	0.31	0.81**
(9) Manganese	-0.78**	0.92**	-0.35	-0.58**	-0.23	-0.66**	0.16	-9.41	--	0.60*
(10) Iron	-0.79**	0.79**	0.00	-0.78**	-0.46	-0.12	0.39	-0.05	0.78**	--

* = significant at 5% level; ** = significant at 1% level.

Note: Values above the main diagonal are for the high marsh; values below the main diagonal are for the low marsh.

75. As a source of inorganic nutrients, a provider of abundant sites for cation sorption, and a fuel for microbially mediated reactions, organic matter is a vital constituent of the soil environment (Buckman and Brady, 1969). Because reduction of manganese and iron to plant-available forms is facilitated by anaerobic bacteria (Turner and Patrick, 1968), strong positive correlations between organic content and these cations might be expected. In fact, most of the correlations were highly negative (Tables 4 and 5). Nixon and Oviatt (1973) noted a close positive correspondence between iron concentration and percent organic matter, but the organic content of their Connecticut marshes averaged less than half that found in the present research. Conceivably, available cations in the highly organic soils of Taskinas Marsh and Bennett's Marsh were rapidly incorporated into microbial biomass, and thus became unavailable to plants. Organic matter was not the sole influence on iron and manganese availability; however, long periods of waterlogging tended to liberate large amounts of available Mn^{2+} and Fe^{2+} (Leeper, 1947); indeed, a strong positive correlation existed between tidal inundation and levels of these cations, particularly in the low marsh zone (Tables 4 and 5).

76. Many species of cations are influenced by the behavior of iron in marsh soils. When surface sediments become aerated during tidal emergence, a number of trace elements, including manganese, co-precipitate with iron in the presence of organic matter (Bloomfield, 1963). Like manganese, iron is readily reduced by microbes. The consistently high positive correlations between iron and manganese

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(Tables 4 and 5) further indicate that the behavior of iron and manganese in marsh soils was closely allied. Iron is also directly involved in the absorption of phosphorus by marsh soils (Jitts, 1959). Hydrated iron oxides provide binding sites for phosphorus ions; ferrous phosphate is believed to be an important mobile compound in reduced soils (Patrick and Khalid, 1974). Iron and phosphate concentrations showed close positive correlation at Taskinas low marsh and Bennett's high marsh, but elsewhere the relationship was either weak or strongly negative. Calcium phosphates are also said to be an important phosphorus source in marsh soils (Broome et al., 1973), but calcium and phosphate correlations were inconsistent.

77. Calcium and magnesium concentrations were highly correlated at both marshes, reflecting the very close resemblance of their spatial profiles (Figures 18 and 19). Laboratory studies indicated that both cations increase in concentration during prolonged submergence, and that their availability is similarly influenced by the decay of organic matter (Robinson, 1930).

78. The foregoing discussion of edaphic interactions raises more questions than it answers. However, it domonstrates that the interactions among sediment variables possess a high degree of complexity and variability--a variability that contributes heavily to the heterogeneity of marsh soils and of their associated vegetation (Gray and Bunce, 1972).

79. Further examination of the habitat intercorrelations (Tables 4 and 5) reveals that the tidal factors (elevation, inundations per year, and hours of inundation) displayed numerous significant

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correlations throughout Bennett's Marsh and at Taskinas low marsh, but
lacked significant correlations at Taskinas high marsh--the same pattern
that typified the plant-habitat correlations (Tables 2 and 3). Of all
the habitat factors considered, only the tide variables possessed sim-
ilar patterns of correlation with both plant factors and other habitat
factors.

80. In regularly inundated areas, both tide vs. habitat and plant
growth vs. habitat correlations were strong; above the reach of the tides
plant growth is no longer closely related to the habitat conditions mea-
sured. This contrast lends circumstantial support to the theory that
tides act to influence plant growth by controlling other aspects of the
marsh habitat. However, it does not diminish the likelihood that inunda-
tion also influences plant growth directly (Hinde, 1954) by imposing
restrictions upon root respiration, nutrient uptake, seed germination, or
other biotic processes. It seems likely that direct and indirect tidal
influences are both important controls on plant growth.

Competition Analyses

81. The present data indicate that plant growth is not closely
related to edaphic conditions in the absence of tidal inundation. Sev-
eral investigators (Johnson and York, 1915; Chapman, 1938; Reed, 1947)
have suggested that competition may affect zonation of marsh plants above
the tide line. Johnson and York (1915) theorized that the landward limit
of occurrence of S. alterniflora is determined primarily by competition
with species, such as S. patens and D. spicata, whose inability to
tolerate prolonged submergence precludes their seaward expansion. Reed

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(1947) amplified the competition hypothesis by suggesting that the accretion of sediments on top of S. alterniflora at the ecotone might confer an advantage upon high marsh species in competing for growing space. Additional mechanisms of competition may be physical, such as inhibition of photosynthesis by shading of leaf surfaces (Ranwell, 1964; Buttery, 1965), or chemical, such as allelopathic interactions. Examination of Figures 5 and 9 reveals that S. patens usually enjoys an advantage in the competition for sunlight.

82. Competitive success or failure is closely tied to habitat phenomena, yet even less is known about plant interactions than about the nature of the marsh habitat. In fact, a thorough quantitative study of plant competition in marshes has never been accomplished.

Gradient Analysis

83. Figures 20 and 21 are examples of community gradient graphs of the study sites. On each figure, values of a single habitat factor were matched with corresponding values of maximum live standing crop data for each species; the standing crop data were expressed as percentages of the largest value. Lines were drawn to indicate patterns of change in standing crop (y-axis) over the range of the particular habitat factor (x-axis). Each line represents a two-point running mean of the data points.

84. The extent to which a given habitat factor influences the segregation of the two communities can be estimated by the degree of isolation of the growth maximum of S. alterniflora (low marsh) from the growth maxima of S. patens and D. spicata along the habitat axis.

73
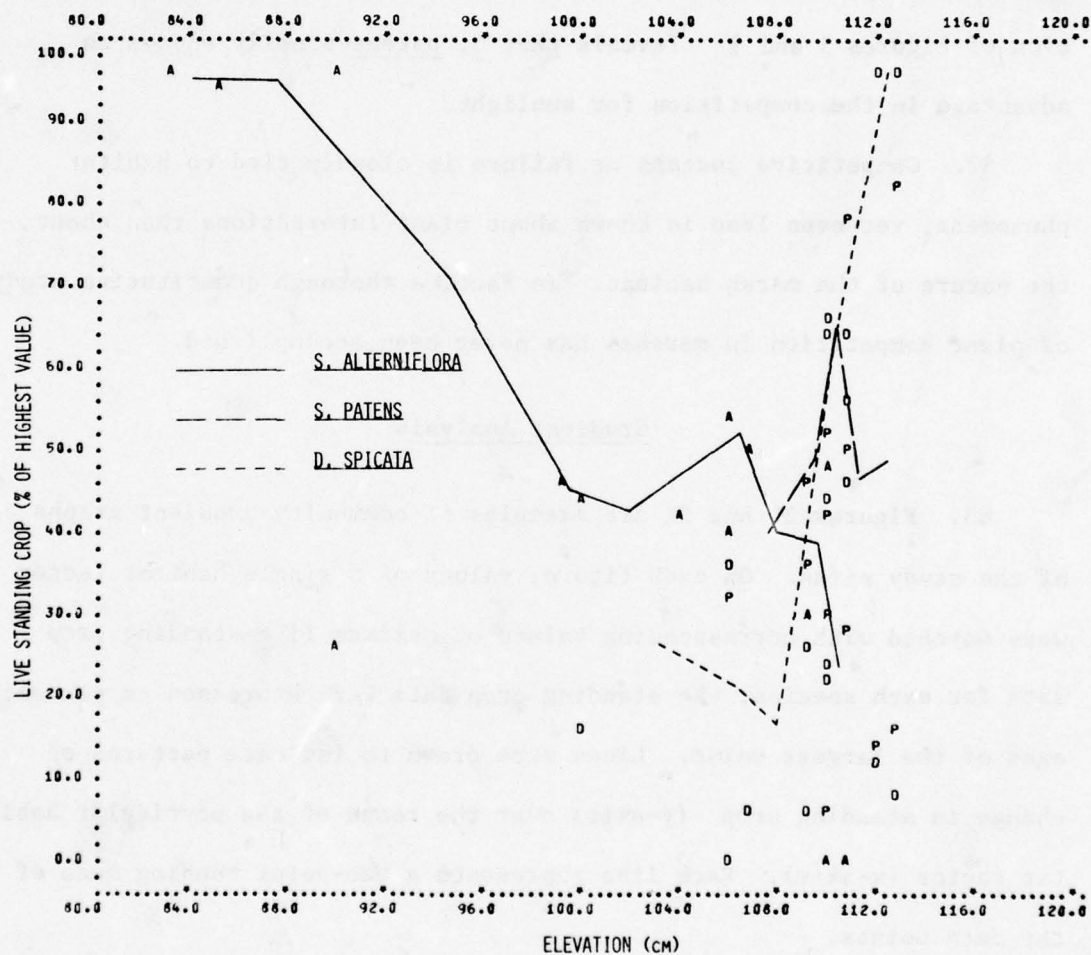
a. Taskinas Marsh

Figure 20. Community gradient plots of live standing crop vs. elevation at (a) Taskinas Marsh and (b) Bennett's Marsh (sheet 1 of 2).

LIVE STANDING CROP (% OF HIGHEST VALUE)

80.0   84.0   88.0   92.0   96.0   100.0   104.0   108.0   112.0   116.0   120.0

100.0

90.0

80.0

70.0

S. ALTERNIFLORA

60.0

S. PATENS

50.0

D. SPICATA

40.0

30.0

20.0

10.0

0.0

80.0   84.0   88.0   92.0   96.0   100.0   104.0   108.0   112.0   116.0   120.0

ELEVATION (CM)
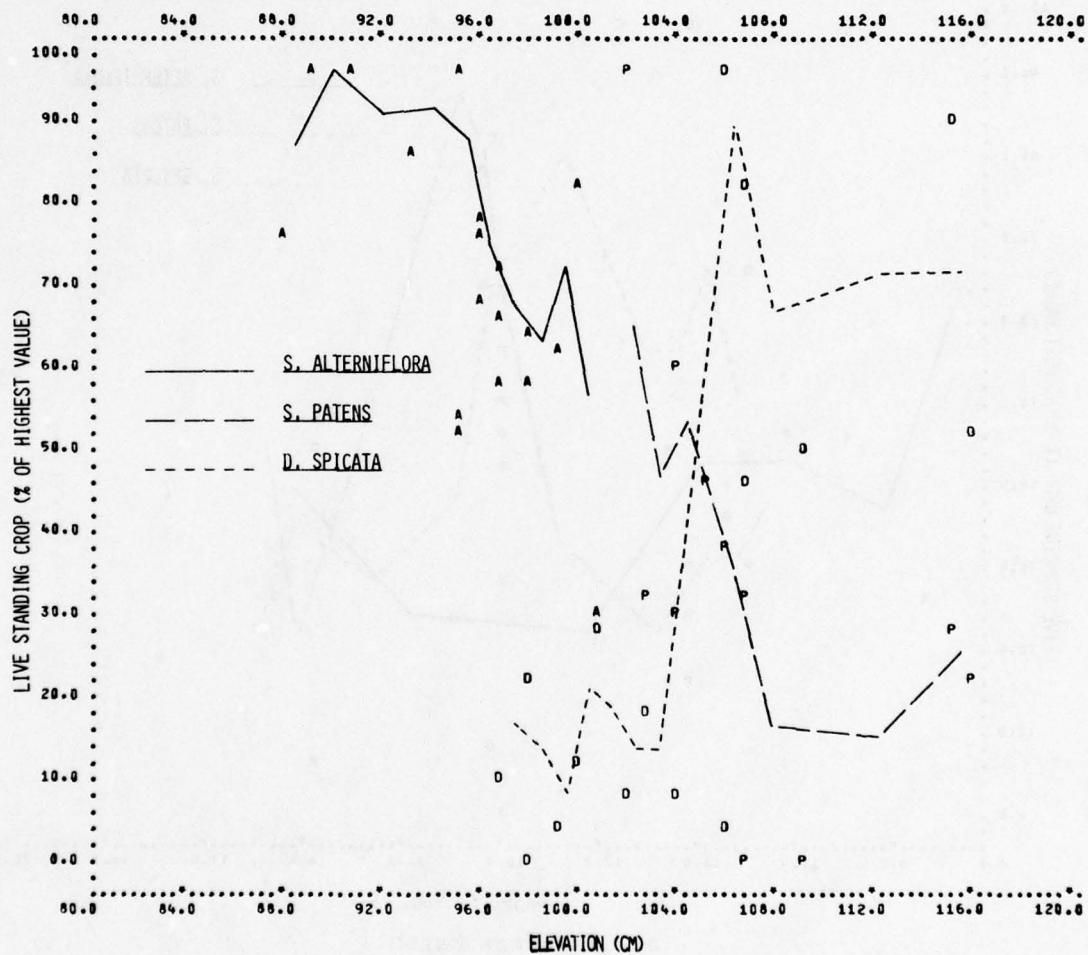
b. Bennett's Marsh

Figure 20   (sheet 2 of 2).
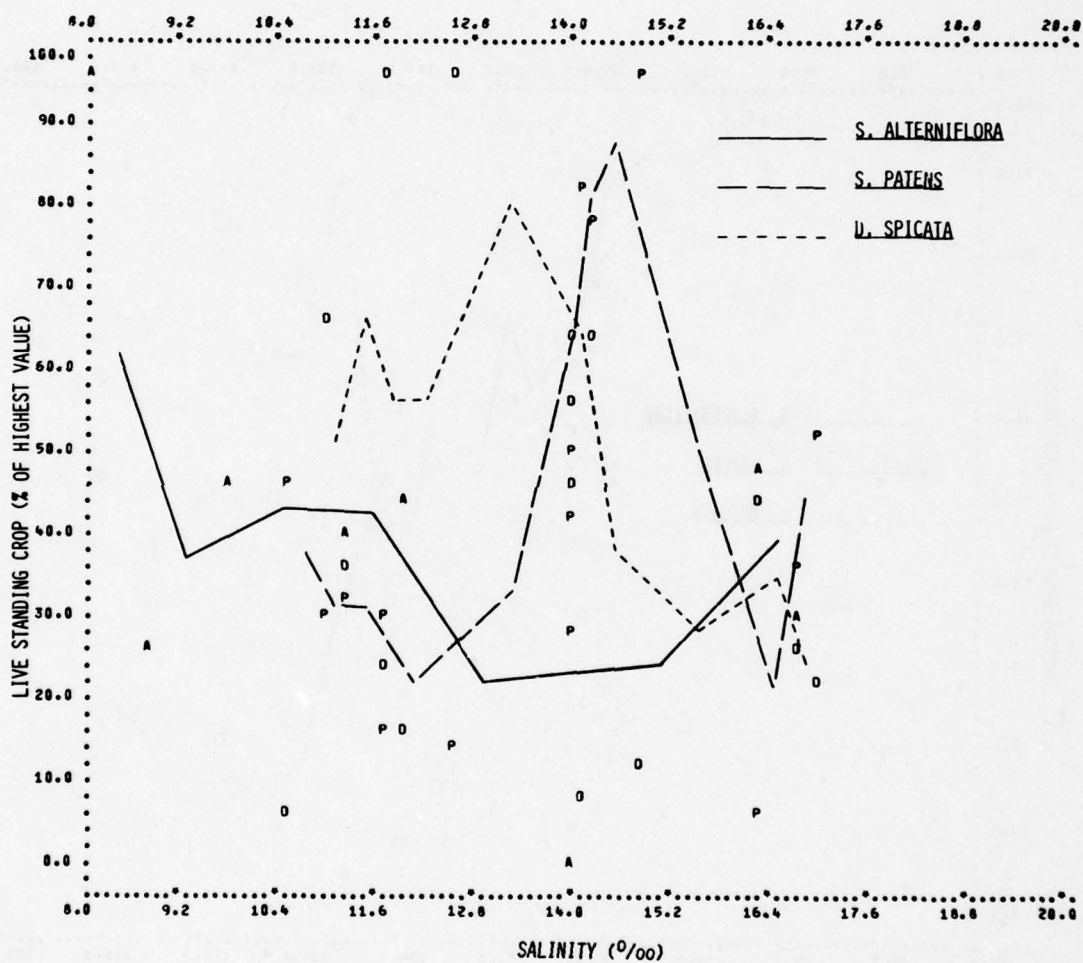
a. Taskinas Marsh

Figure 21. Community gradient plots of live standing crop vs. salinity at (a) Taskinas Marsh and (b) Bennett's Marsh (sheet 1 of 2).
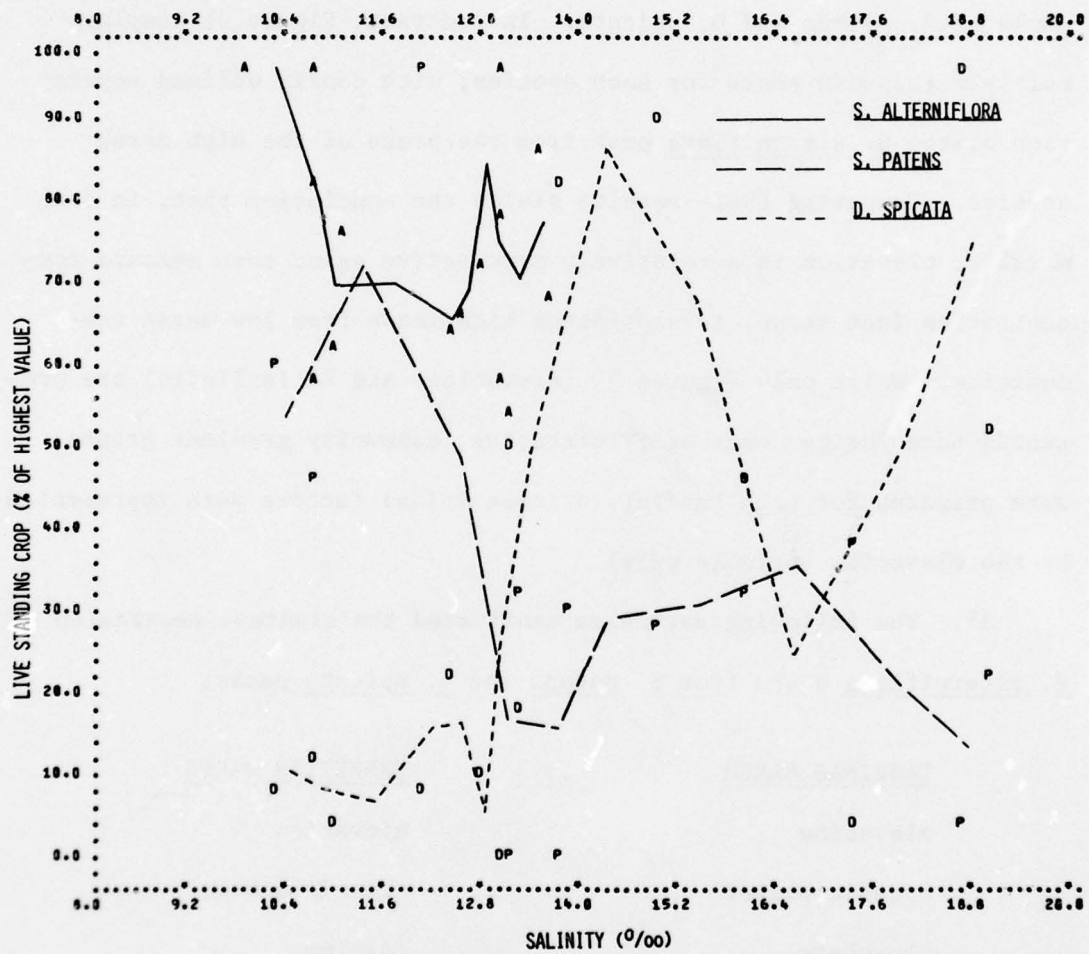
b. Bennett's Marsh

Figure 21 (sheet 2 of 2).

Because the scales of the habitat factors have not been normalized, this evaluation is somewhat arbitrary; nevertheless, the patterns represented can be compared qualitatively. For example, Figure 20 shows clearcut separation of the S. alterniflora response peak from the peaks of S. patens and D. spicata. In contrast, Figure 21 displays multiple response peaks for each species, with poorly defined separation of the S. alterniflora peak from the peaks of the high marsh species. Comparing these results yields the conclusion that, in both marshes, elevation is a relatively more active agent than ammonia concentration (not shown) in separating high marsh from low marsh communities. While only Figures 20 (elevation) and 21 (salinity) are presented here for purposes of illustration, community gradient graphs were prepared for each habitat variable (tidal factors were represented by the elevation variable only).

85. The following variables manifested the clearest separation of S. alterniflora peaks from S. patens and D. spicata peaks:

TASKINAS MARSH	BENNETT'S MARSH
elevation	elevation
organic matter	organic matter
phosphate	calcium
manganese	magnesium
	manganese
	iron

The community gradient technique thus singled out the above factors as the most influential in dividing the vegetational zones.

86. A second phase of gradient analysis, the complex gradient approach (Whittaker, 1967), arrayed pairs of these selected habitat factors on opposing axes and plots corresponding standing crop data in habitat spaces. Standing crop data were plotted on a two-level rating scale:

optimal - 50 percent or more of maximum live standing crop

sub-optimal - less than 50 percent of maximum live standing

crop

This two-part scale superseded the "percent" scale used on community gradient graphics.

87. The object of the complex gradient analysis was to pinpoint pairings of habitat factors that most clearly separate the optimal ranges of $\underline{S}$. $\underline{patens}$ and $\underline{D}$. $\underline{spicata}$ from that of $\underline{S}$. $\underline{alterniflora}$.

88. Illustrative examples of complex gradient plots are presented for Taskinas Marsh (Figures 22 and 23) and Bennett's Marsh (Figures 22 and 24). In each plot, the optimal portion of a species' range is shaded by parallel lines, while the sub-optimal range is merely outlined.

89. At Taskinas Marsh, the combination of elevation and organic matter (Figure 22) appeared to produce the clearest separation of high marsh and low marsh optima along both axes. Other combinations of selected factors, such as manganese and phosphate (Figure 23), show a greater degree of overlapping of optima. Similarly, only the graph of elevation and organic matter at Bennett's Marsh (Figure 22) clearly separated the $\underline{S}$. $\underline{alterniflora}$ optimum from the optima of the high

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19.0   14.0   18.0   22.0   26.0   30.0   34.0   38.0   42.0   46.0   50.0

120.0

116.0

112.0

108.0

104.0

ELEVATION (CM)

100.0

96.0

92.0

88.0

84.0

80.0

10.0   14.0   18.0   22.0   26.0   30.0   34.0   38.0   42.0   46.0   50.0

% ORGANIC MATTER

SPECIES RANGES :

——————— S. ALTERNIFLORA

– – – – – – S. PATENS

- - - - - - D. SPICATA

MAXIMUM STANDING CROP :

S. ALTERNIFLORA

S. PATENS

D. SPICATA
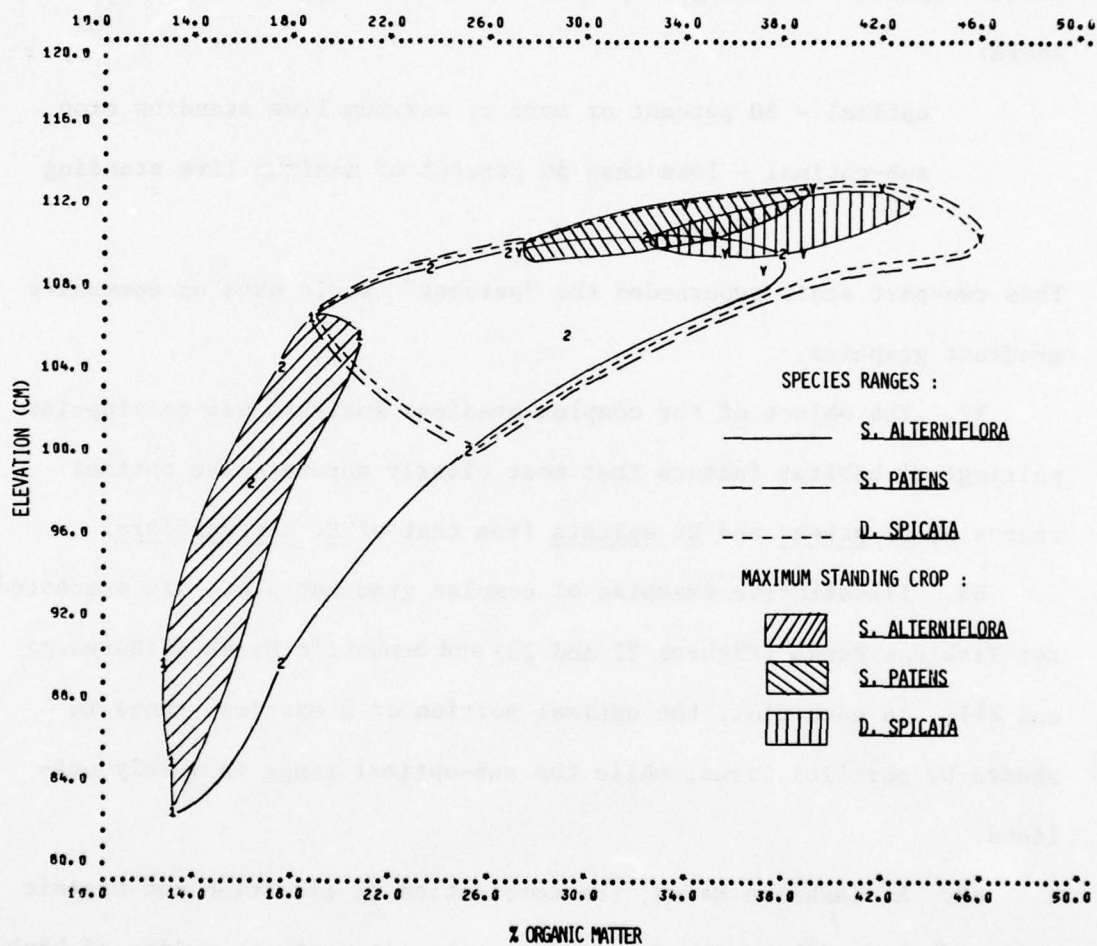
a.   Taskinas Marsh

Figure 22.   Complex gradient plots of live standing crop vs.
organic matter and elevation at (a) Taskinas
Marsh and (b) Bennett's Marsh (sheet 1 of 2).
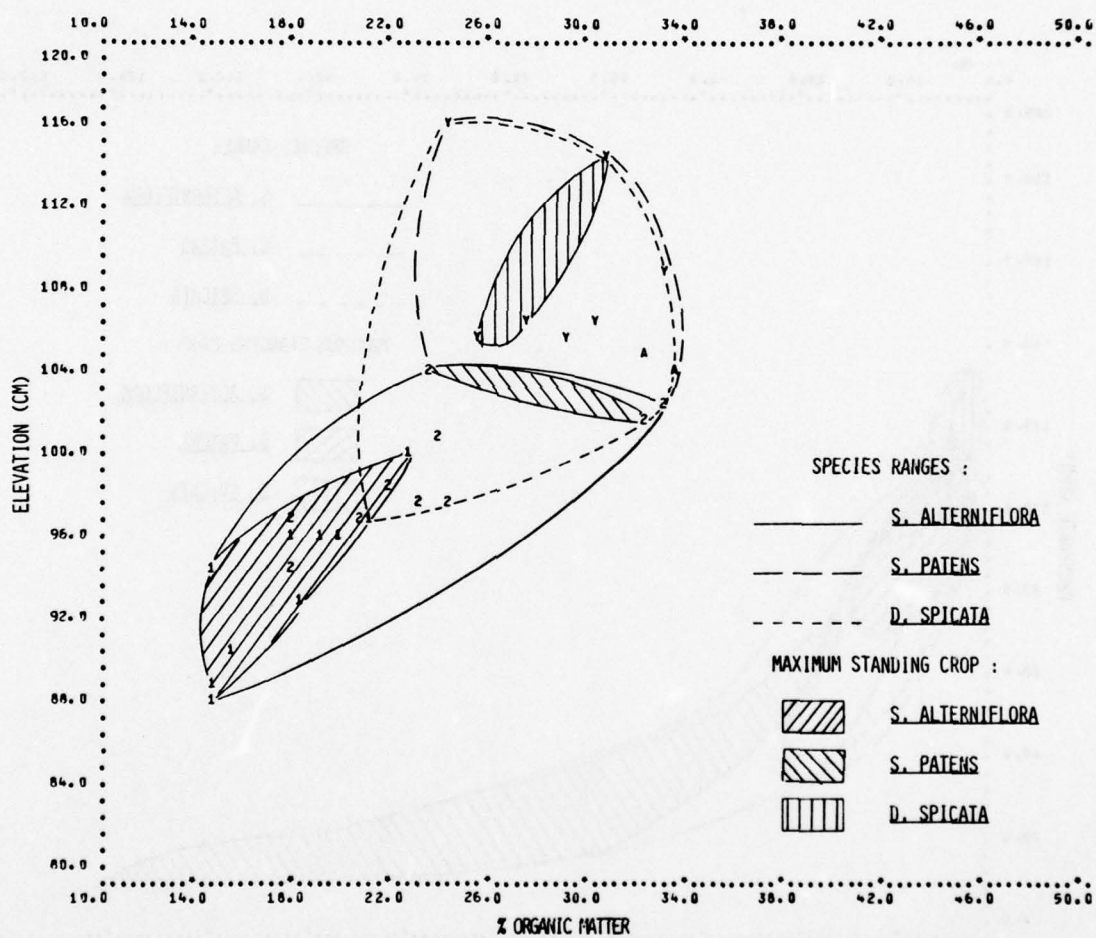
b. Bennett's Marsh

Figure 22 (sheet 2 of 2).
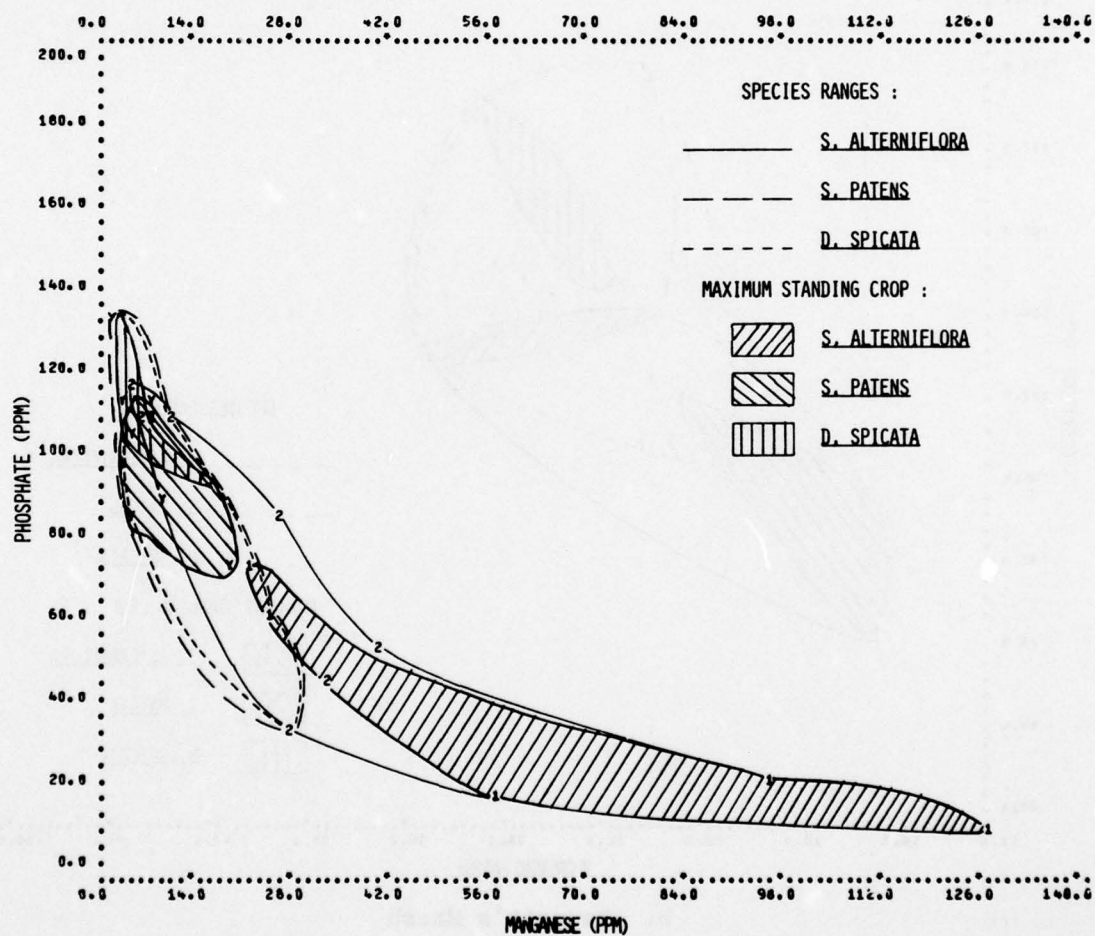
Figure 23. Complex gradient plots of live standing crop vs. manganese and phosphate at Taskinas Marsh.
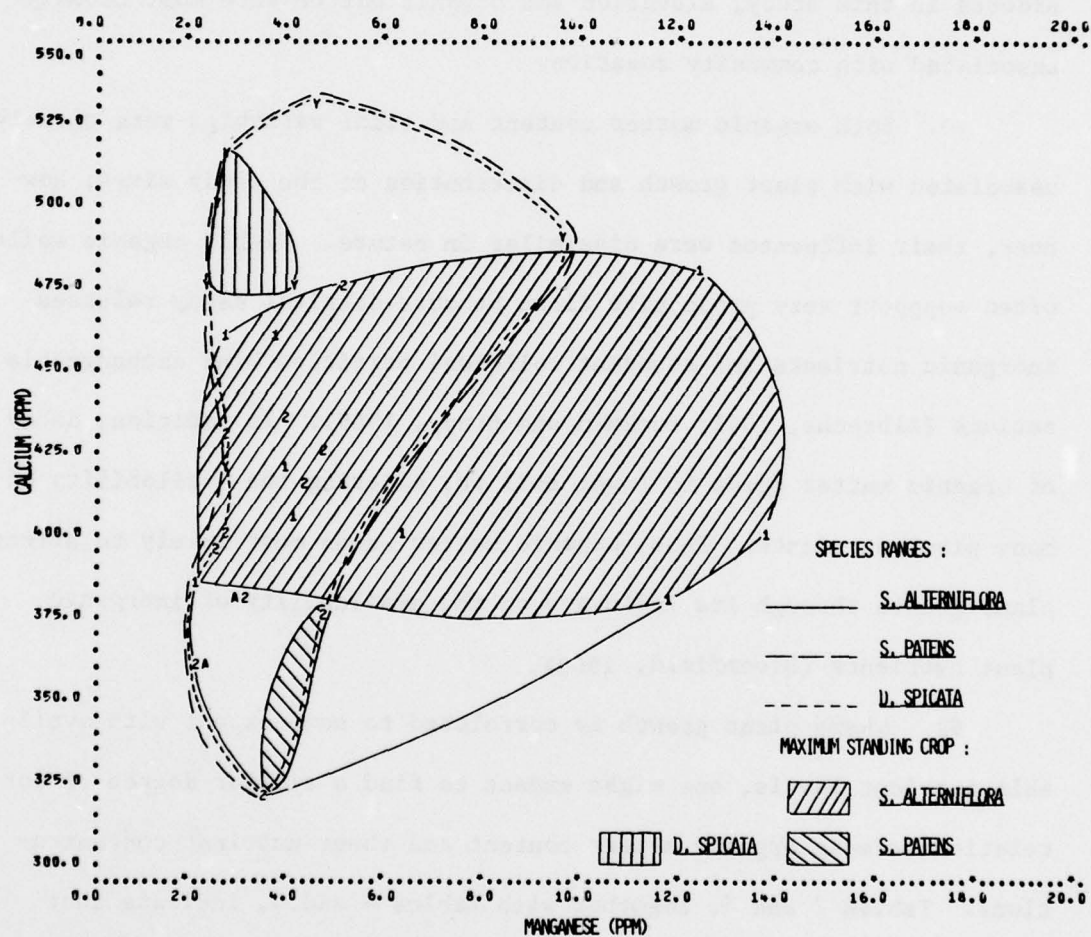
Figure 24. Complex gradient plots of live standing crop vs. manganese and calcium at Bennett's Marsh.

marsh species along both axes. The consistency of the results between the plot of manganese and calcium at Bennett's Marsh (Figure 24) exemplified factor combinations with overlapping low marsh and high marsh optima and led to the conclusion that, among the habitat factors considered in this study, elevation and organic matter were most closely associated with community zonation.

90. Both organic matter content and tidal variables were closely associated with plant growth and distribution at the study sites; however, their influences were dissimilar in nature. Highly organic soils often suppport very productive flora because detrital decay releases inorganic nutrients and abundant colloidal particles bind exchangeable cations (Albrecht, 1941; Buckman and Brady, 1969). In addition, decay of organic matter tends to lower soil pH, altering the availability of many plant nutrients. Thus, organic matter seems most likely to affect plant growth through its influence on the availability of inorganic plant nutrients (Bloomfield, 1963).

91. Where plant growth is correlated to some extent with available nutrient levels, one might expect to find a similar degree of correlation between organic matter content and these nutrient concentrations. Tables 2 and 3, together with Tables 4 and 5, indicate that this correspondence was found in the low marsh zones, but not in the high marsh zones. Considering all three major plant species together, then, the influence exerted by organic matter upon plant growth appears to be somewhat inconsistent. As noted previously, tide-habitat correlation patterns are paralleled by tide-plant growth correlation

patterns. Comparing tide and organic matter correlation patterns in this manner suggests that tidal influences may be the more pervasive. Furthermore, since sedimentation rate, a determinant of the organic matter content of marsh soils, is itself largely a function of the degree of tidal inundation (Broome et al., 1973), it seems apparent that tides exert some control over organic matter content. The sum of the evidence in this project, therefore, appears to point toward tidal inundation as the major controlling influence upon plant growth and zonation.

92. Prevalence of the close relationship between tide factors and vegetation tends to obscure major differences between the marshes. Certain habitat factors were significantly correlated with plant growth at only one marsh (Tables 2 and 3); interrelationships among habitat factors (Tables 4 and 5) also varied between Taskinas Marsh and Bennett's Marsh.

93. Even the zonations of species with regard to tidal inundation were somewhat dissimilar. Table 6 contrasts the two marshes in terms of species tolerance to tidal inundation. The two inundation parameters were calculated only for the extremes of species distribution that fell within the sample zone; that is, the landward limit of S. alterniflora and the seaward limits of S. patens and D. spicata.

94. Inundation tolerances were uniformly greater at Bennett's Marsh than at Taskinas Marsh. S. alterniflora tolerated a minimum of six inundations per year at Bennett's, but survived with no inundation at Taskinas. Both S. patens and D. spicata survived considerably more inundation at the lower limits of their range at Bennett's than

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Table 6

Limits of Tolerance to Tidal Inundation for Three Species of
Marsh Grasses at Taskinas Marsh and Bennett's Marsh

| Species | Inundation Events per Yr. | | | | Hrs. of Inundation per Yr. | | | |
| | Taskinas | | Bennett's | | Taskinas | | Bennett's | |
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
S. alterniflora	--	0	--	6	--	0	--	3.5
S. patens	8	0	17	--	6.5	--	22	--
D. spicata	8	--	41	--	6.5	--	65	--

Note: Max. = maximum number of events recorded
       Min. = minimum number of events recorded
       --   = not measured within sampling sites

at Taskinas. While $\underline{D}$. spicata tolerated several times more inundation than $\underline{S}$. patens at Bennett's, the two species showed the same tolerance limits at Taskinas.

95. It should be noted, however, that annual estimates of tidal inundation are subject to inaccuracy from several environmental sources, including alteration of the tidal prism by wind, hindrance of tidal waters by physical resistance of the vegetation, and variability of sediment drainage rates (Kurz and Wagner, 1957). Inundation of Taskinas high marsh, though not predicted, has been observed when high tides coincide with strong northwest winds (J. Pickral, 1976, personal communication[*]).

96. Despite estimation errors, tidal tolerances of each plant species appeared to differ markedly between the two marshes. Assuming that a given species has the genetic potential for response to tidal inundation in both marshes (Mooring et al., 1971), differences in response might be explained by the divergent past histories of the marshes. As discussed previously, Taskinas Marsh is presently undergoing a "drowning" phase, while Bennett's Marsh appears to be building upward by sediment accretion. A gradually sloping foreshore, such as at Bennett's Marsh, is frequently associated with a young, expanding marsh (Redfield, 1972), while the steeper foreshore at Taskinas is more typical of a mature marsh (Stevenson and Emery, 1958). The difference profoundly affects the extent of tidal inundation (Figure 11). The

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[*]J. Pickral, 1976, Dept of Environmental Sciences, University of Virginia, Charlottesville, VA 22903.

absence of predicted inundation in Taskinas high marsh may result from a relatively recent high stand of the marsh, as evidenced by the presence of scattered dead I. frutescens among the high marsh grass. In other words, the contemporary tidal regime of the high marsh was conditioned by this past episode as well as by the current drowning phase.

97. In mature marshes, particularly, vegetational succession in response to changing relative sea level experiences time lags. Reed (1947) suggested that, in an aggrading marsh, S. alterniflora stems buried by accumulating sediments may remain alive for some time, since their roots continue to exist under relatively unchanged conditions. Eventually, the high marsh species encroaching on the new sediments smother the S. alterniflora beneath them, and the transition is completed. Similarly, the retrogressive succession accompanying rising relative sea level (Kurz and Wagner, 1957) often requires that an invading species (e.g., S. alterniflora at Taskinas Marsh) establish itself among a dense, fibrous mat of high marsh vegetation. Ranwell (1964) observed that competition from Spartina townsendii appeared to retard the advance of invading species, even when habitat conditions would have permitted the invaders to expand more rapidly. Pre-existing vegetation thus may possess a competitive advantage by virtue of its physical occupation of the growing space, enabling it to persist for some time despite an increasingly unfavorable habitat. The equilibration time of marsh vegetation during periods of change in relative sea level may significantly modify the relationship between vegetational distribution and tidal inundation.

PART VI: MONITORING RESULTS

98. As the monitoring equipment was built, it was tested success-
fully in the laboratory; in the harsher environment of the salt marsh,
however, unforeseen problems arose. Throughout the field monitoring
phase, the equipment was plagued by component failure of varying
severity. The initial difficulties were most serious; failure of one
or more components would induce problems in others, and the system's
performance would totally deteriorate. Chief among these early prob-
lems were loss of amplifiers due to electronic failure, and disappear-
ance of a transmitted signal or shorting out due to water leakage
around the submersible connectors.

99. When the amplifiers malfunction, the unit frequently sets up
an overvoltage. The recorder normally receives an input of 0.0 to 1.0
v-d.c.; any higher voltage produces erroneous records on the channel in
which the overvoltage occurs and in adjacent channels as well. A suffi-
ciently high overvoltage damages the recorder itself. Ultimately, volt-
age regulators were installed on the outputs of all amplifiers to pre-
vent overvoltages, but many records were lost before this problem was
alleviated.

100. The other major problem, which was not fully resolved,
involved the shorting out of signals between the amplifiers and the
junction boxes. The major cause of this problem proved to be leakage
in the submersible cable connectors. Since it was frequently necessary
to carry the equipment several hundred meters to the study site, the
units were designed in a modular fashion to facilitate handling assembly

on the marsh. Despite careful handling, bits of sediment and droplets of salt water frequently became attached to exposed connectors and were not completely removed by a final cleaning prior to assembly of the connectors. Any trace of water or salt on the connectors allowed the voltage to leak, either to ground or to another connector. This leakage periodically caused erroneous behavior which was often perplexing and difficult to trace. Despite the host of electronic problems in the system and the consequent lack of complete records, the results from the monitoring system were quite encouraging. The main value of this part of the project was the demonstration of the feasibility of recording small time interval variations in sedimentary parameters and relating these variations to plant distribution.

101. The most complete set of data collected with the system was collected between 25 and 28 November, 1975 at Taskinas Creek; portions of this are shown in Figures 25 to 30. The figures depict incoming solar radiation in Taskinas Creek, tidal fluctuation, and pH and temperature at the surface and 10 cm below the sediment surface in several marsh zones. These figures readily show the high degree of variability present in the marsh, and also the difficulty in analyzing this type of continuous data. The curves of solar radiation (Figure 25) and tidal height (Figure 26) were relatively smooth and easy to interpret, since the diurnal periodicity of radiation and semidiurnal nature of the tides were readily apparent. However, graphical analyses of temperature and pH curves is a formidable task, since patterns of behavior are masked by wide variation and signal noise (Figures 27 to 30).

| 2000 | | 2400 | | 400 | | 800 | | 1200 | | 1600 | | 2000 | | 2400 |

4

2000   2400   400   800   1200   1600   2000   2400

HOURS
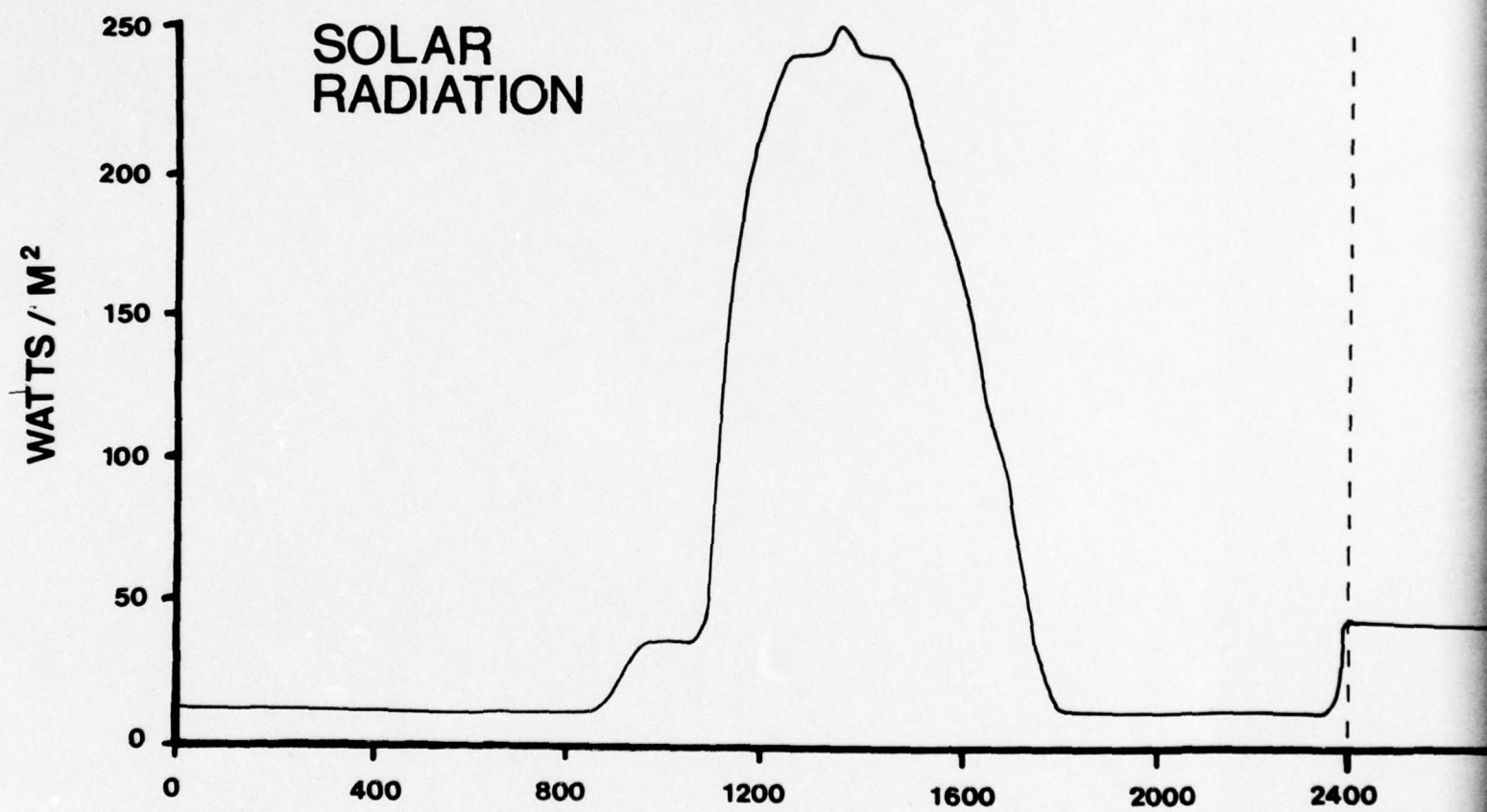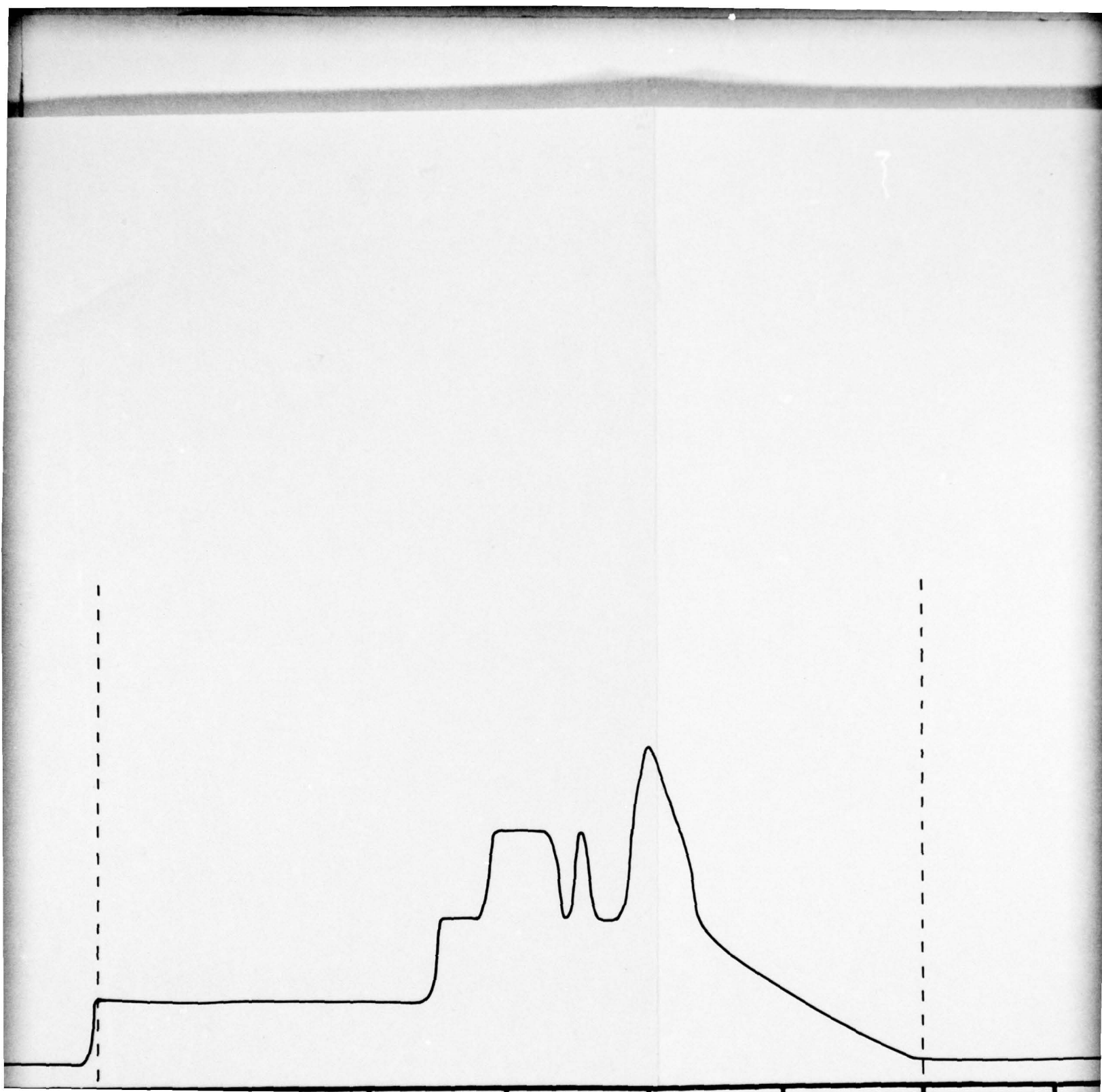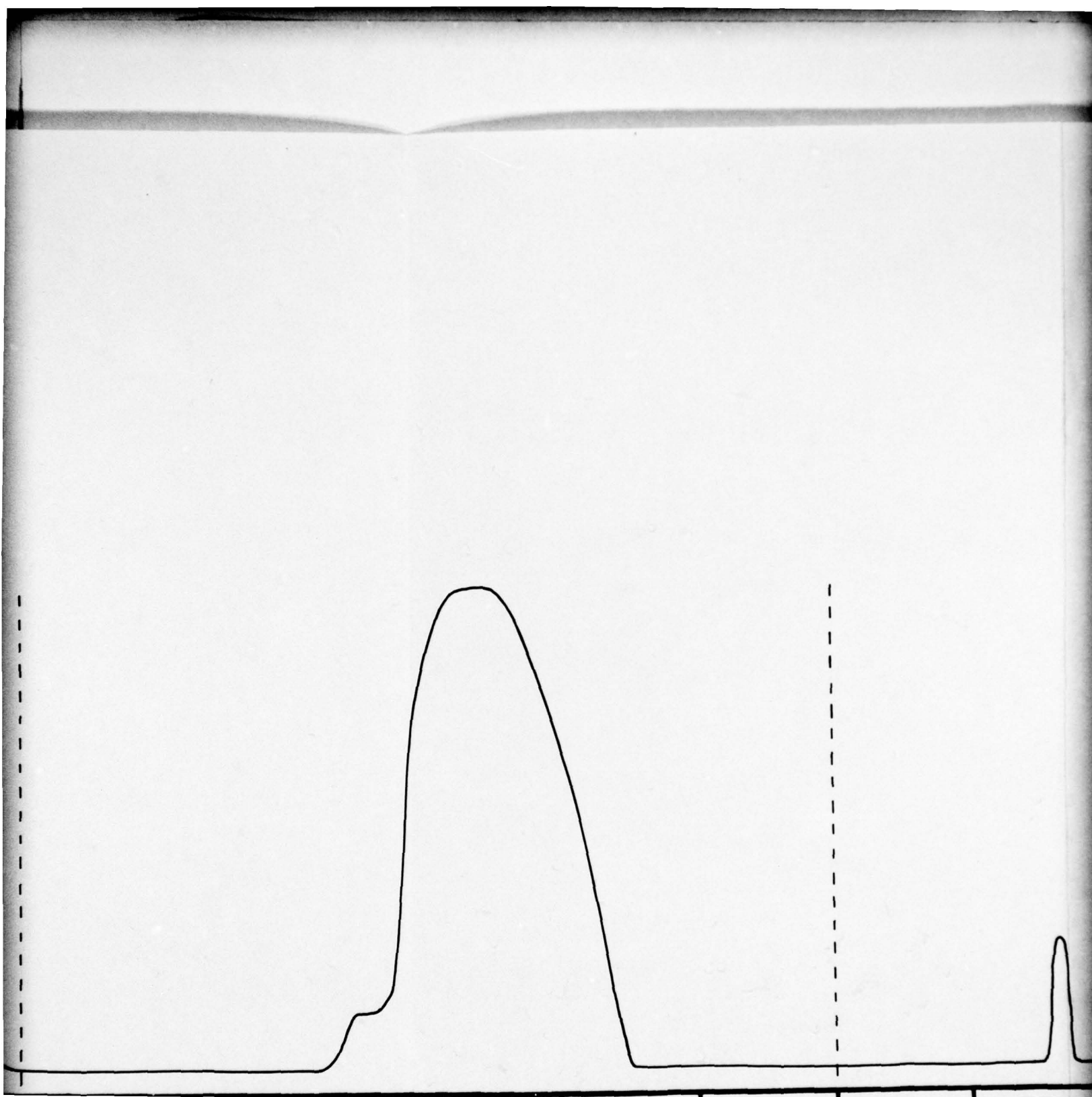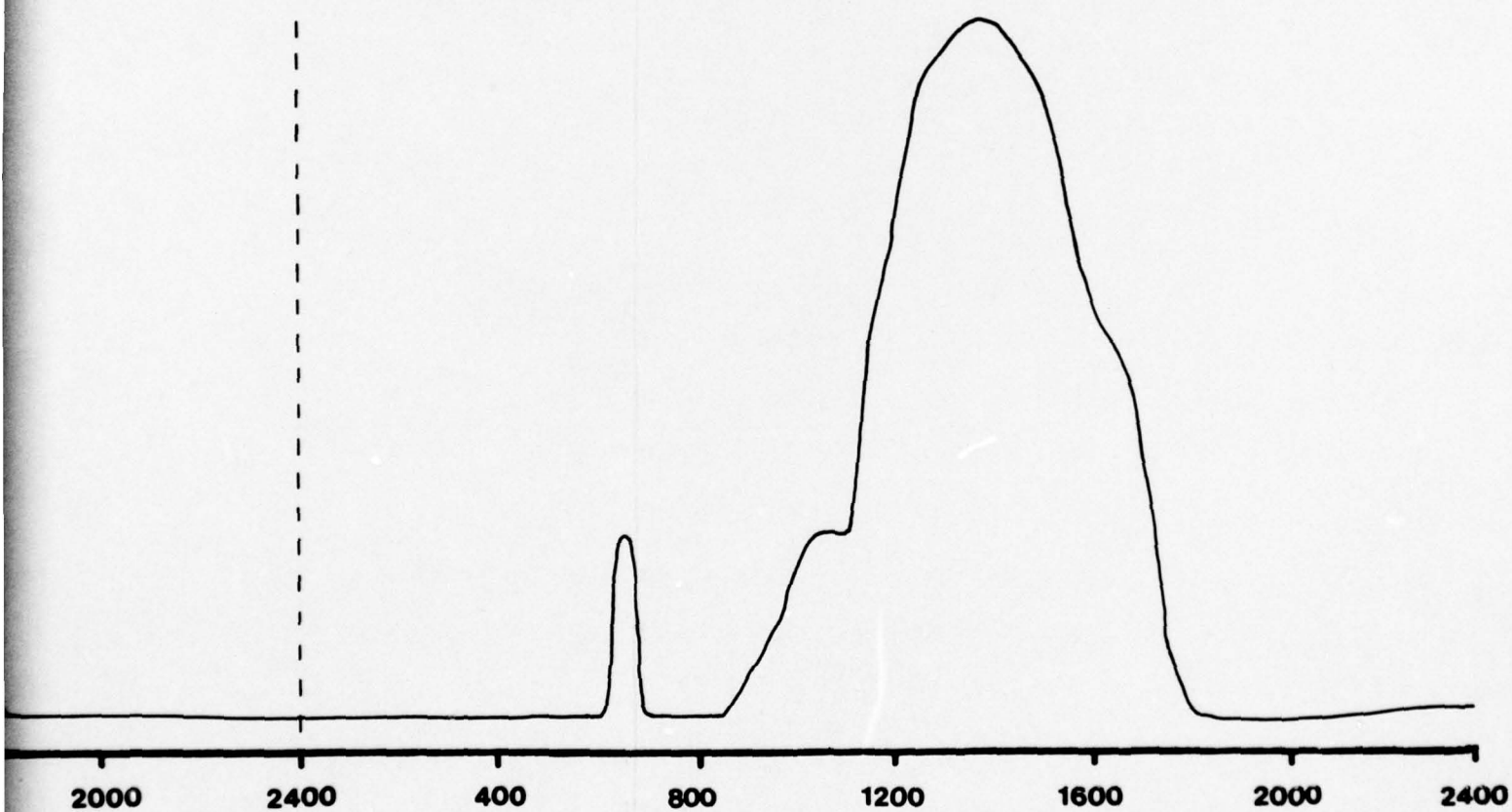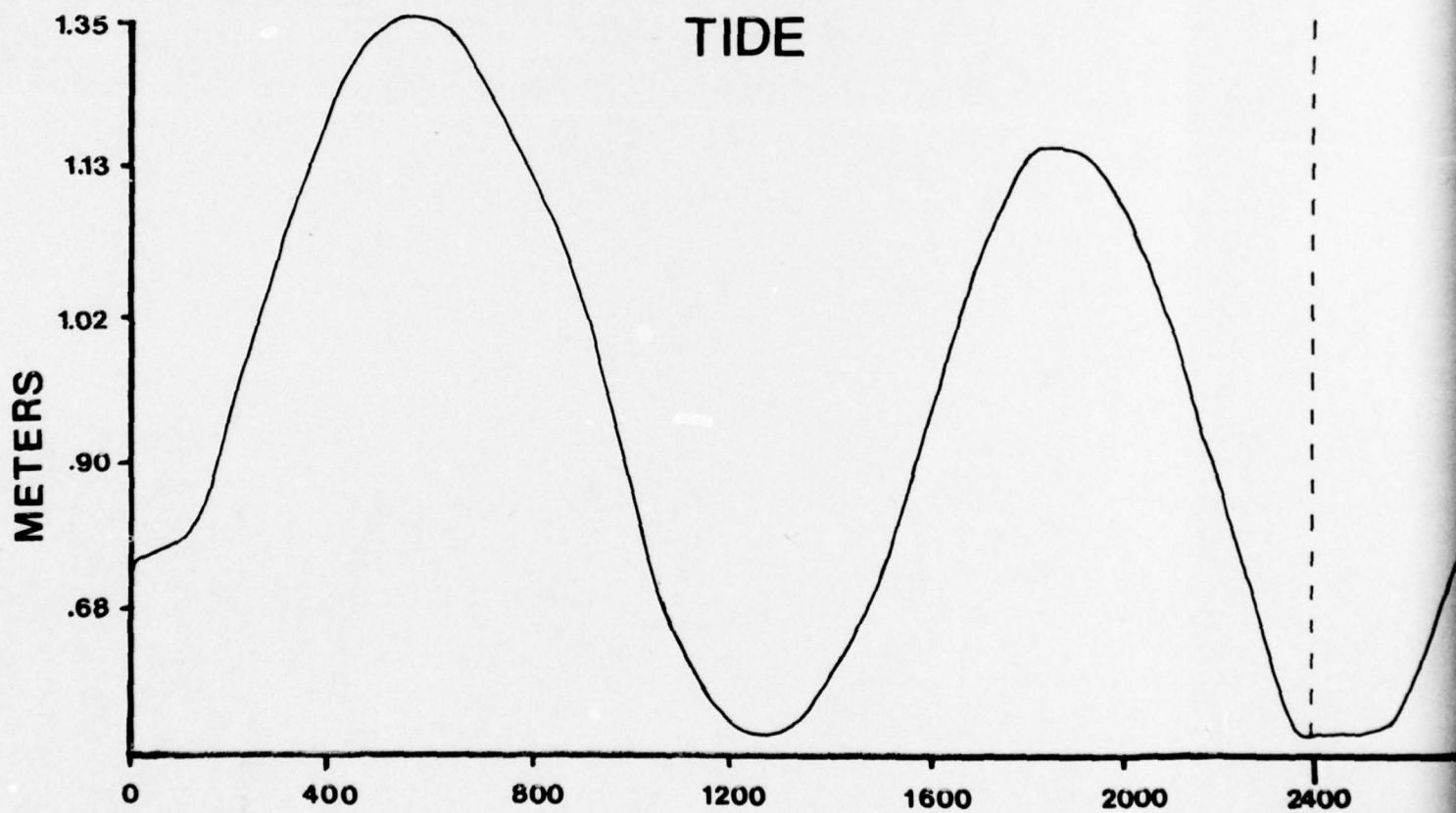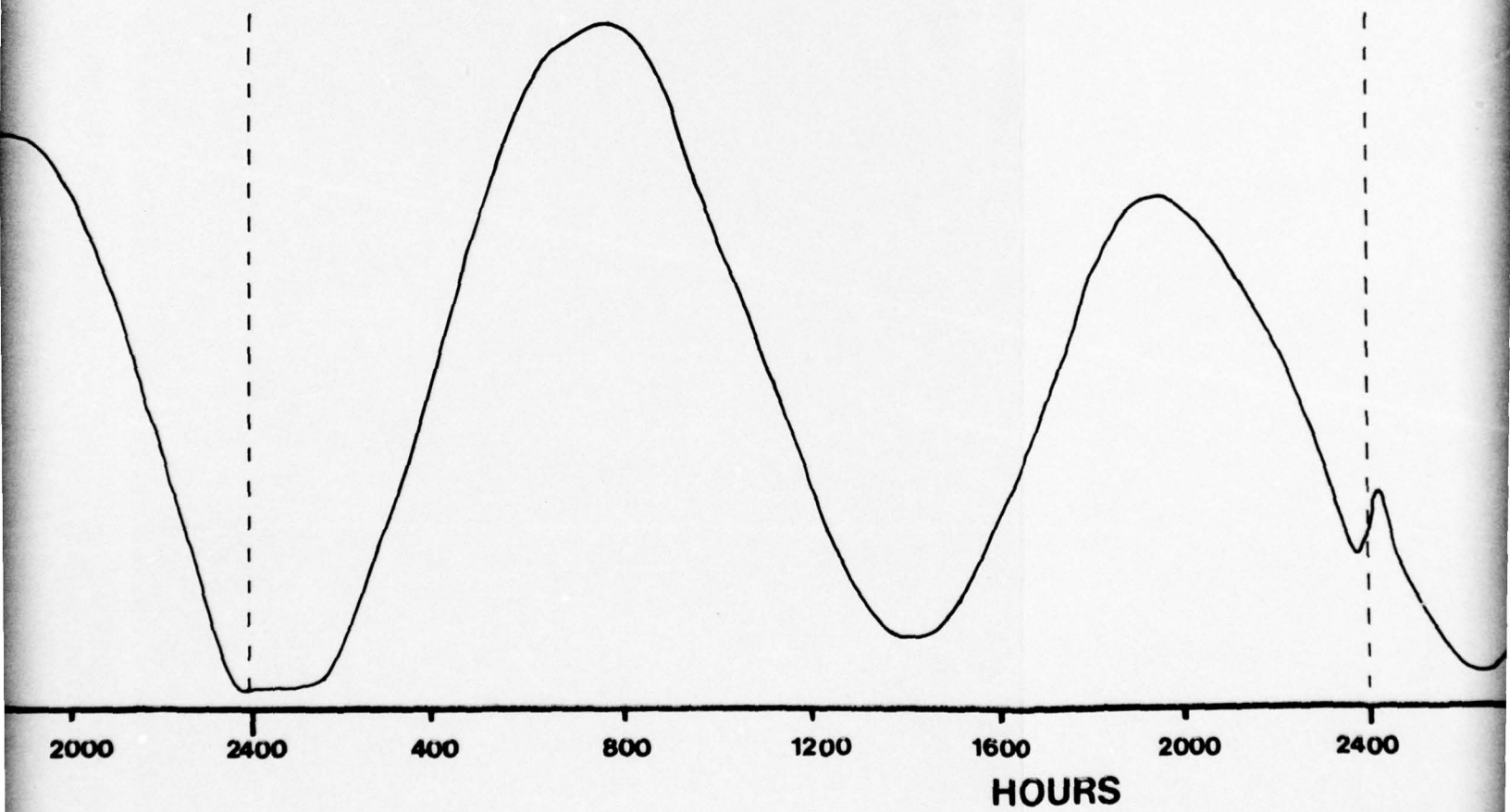
Figure 26. Tidal height at Taskinas Marsh from 2

2000　　　2400　　　400　　　800　　　1200　　　1600　　　2000　　　2400

RS

height at Taskinas Marsh from 25 to 28 November 1975.

| 2000 | 2400 | 400 | 800 | 1200 | 1600 | 2000 | 2400 |

4
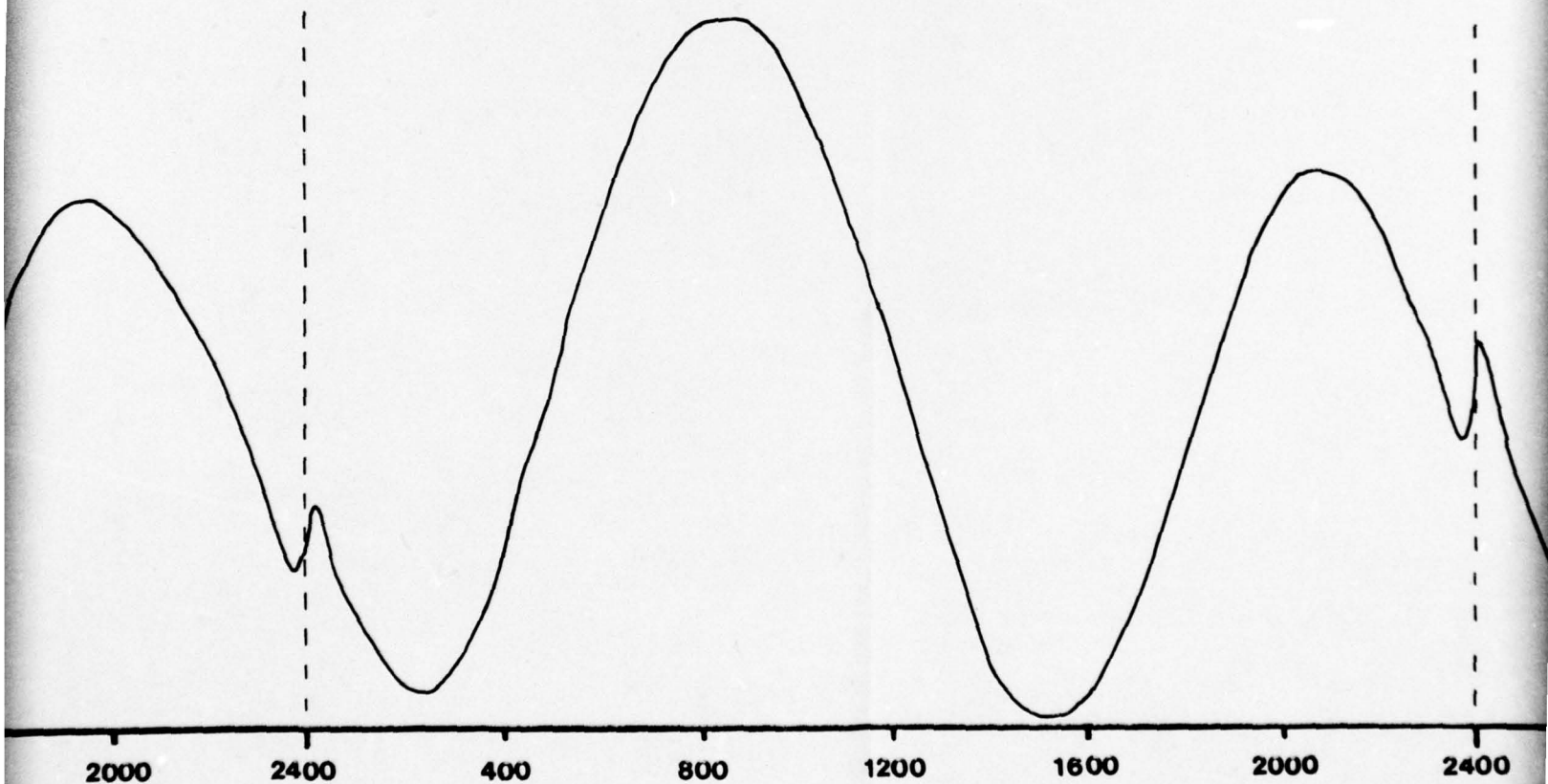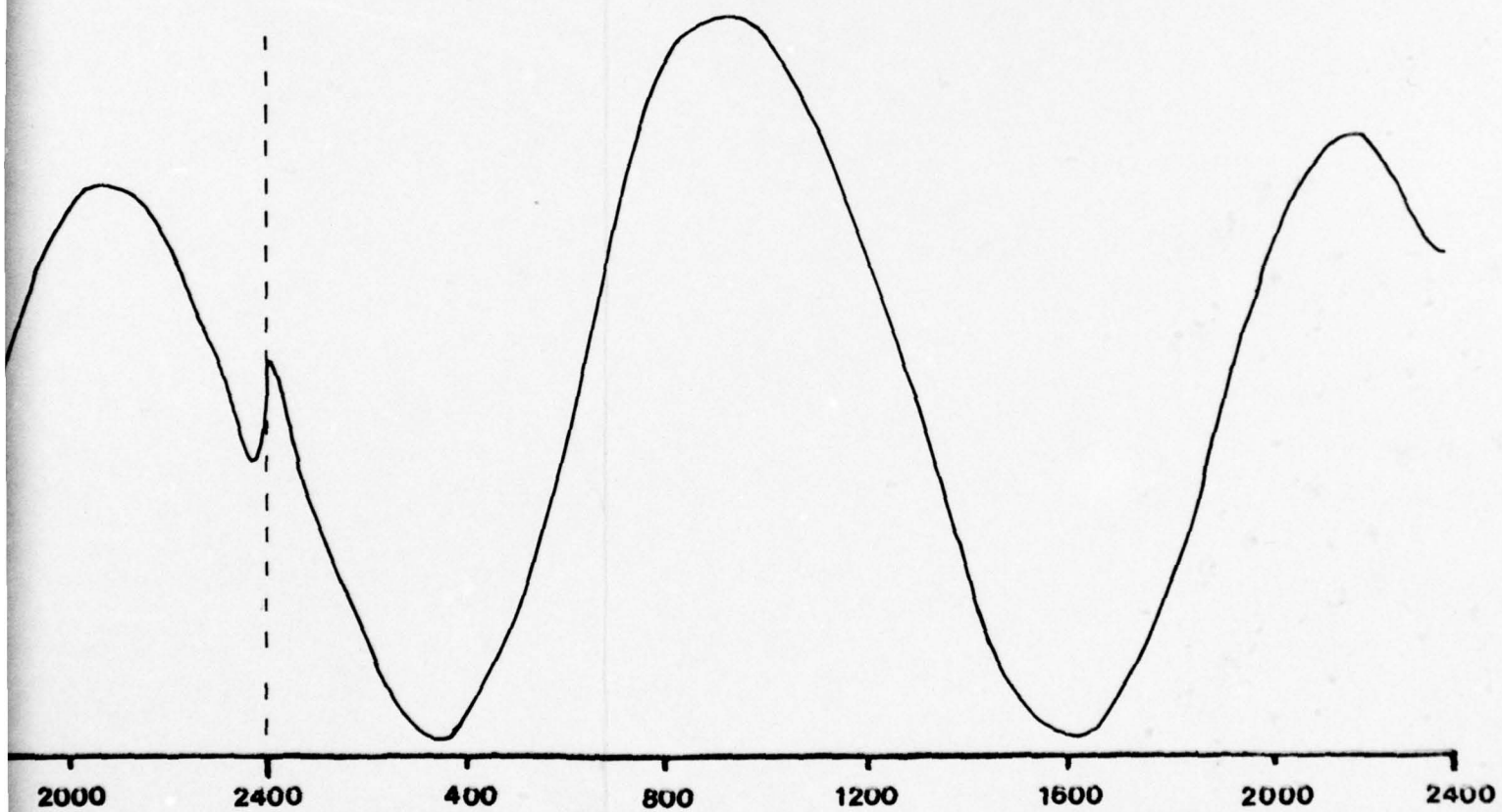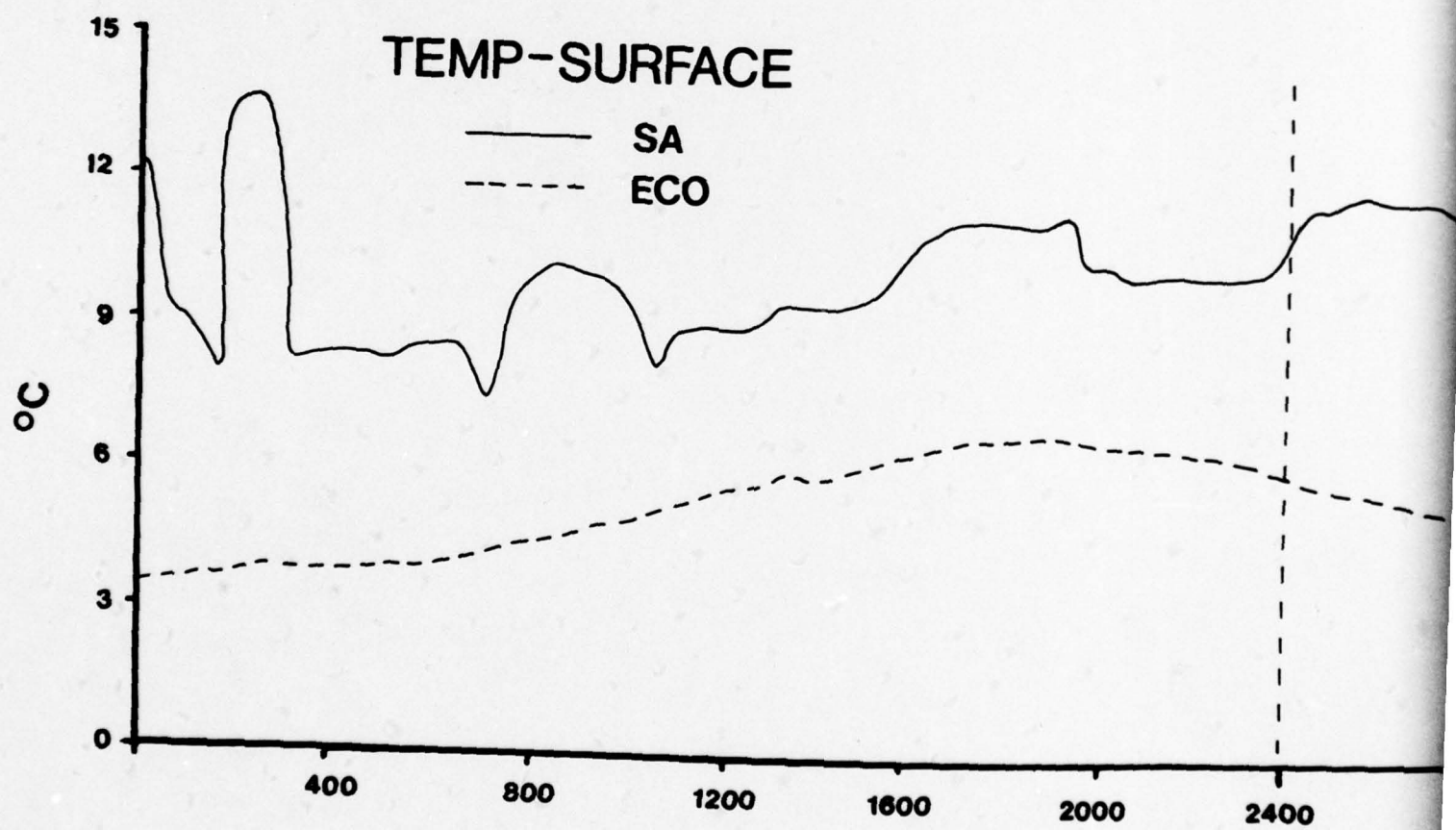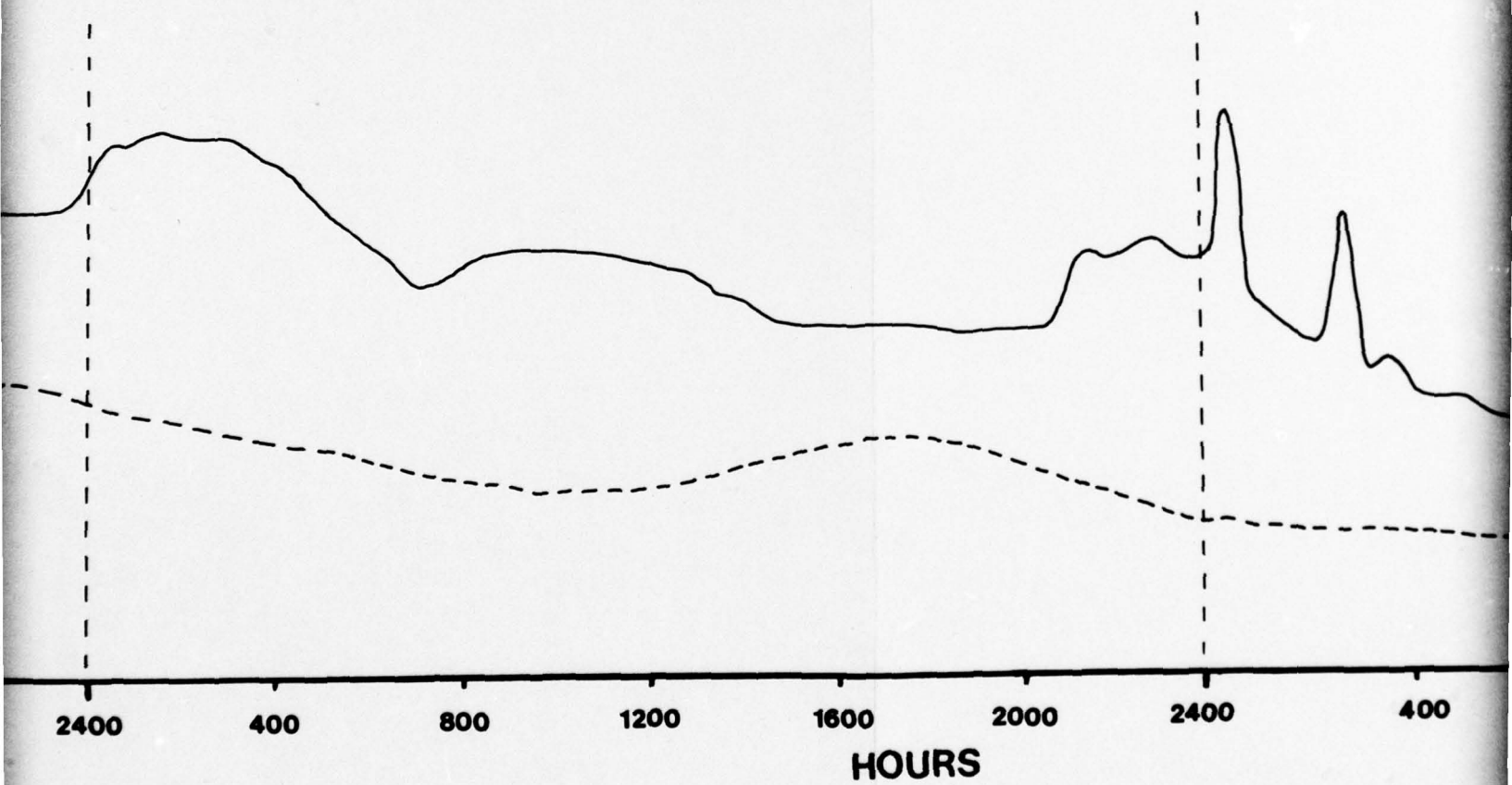
TEMP-SURFACE

Figure 27. Temperature at the sediment surface at Taskinas Marsh from

skinas Marsh from 25 to 28 November 1975.

2000   2400   400   800   1200   1600   2000   2400

4

2000   2400   400   800   1200   1600   2000   2400
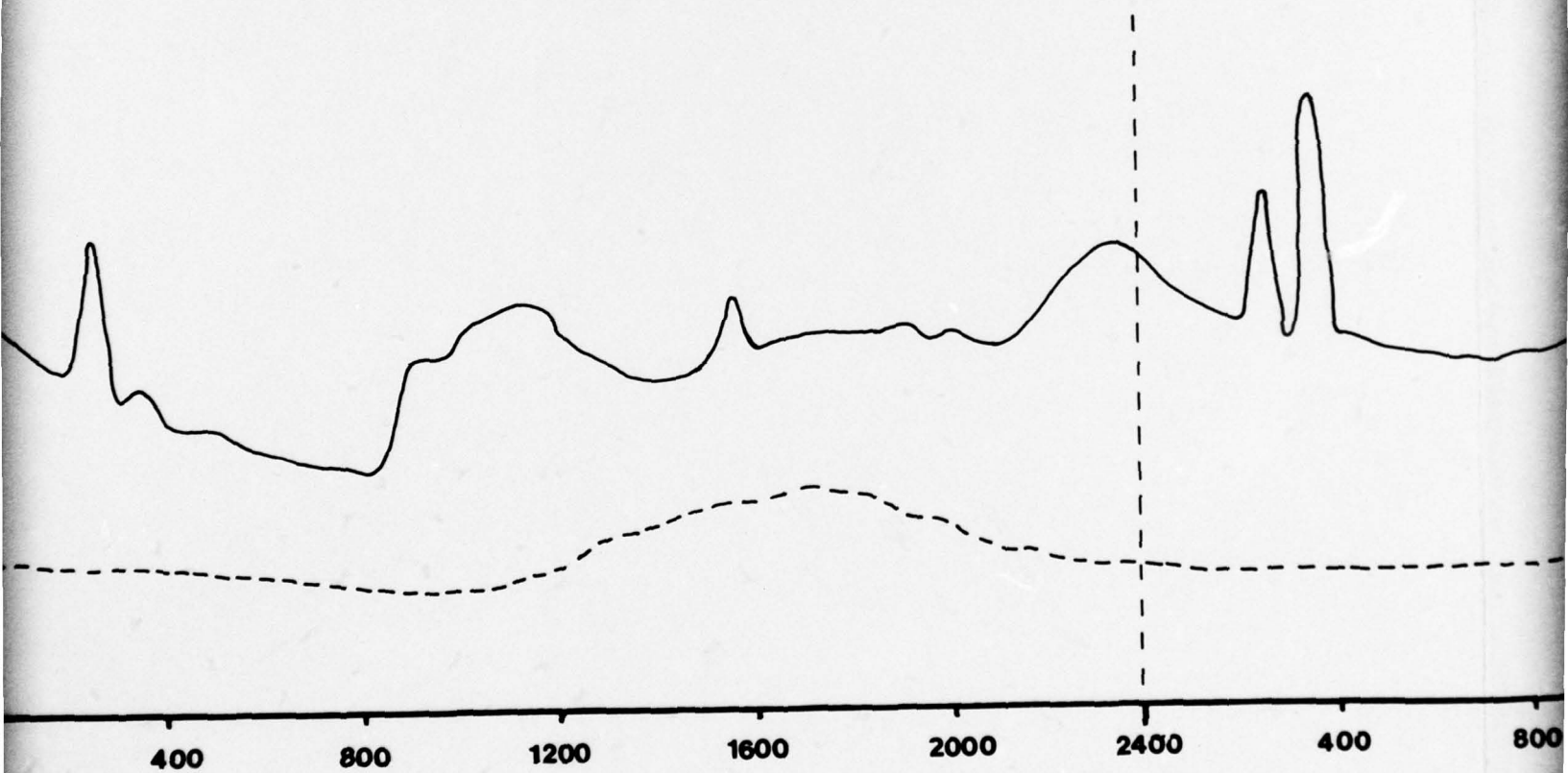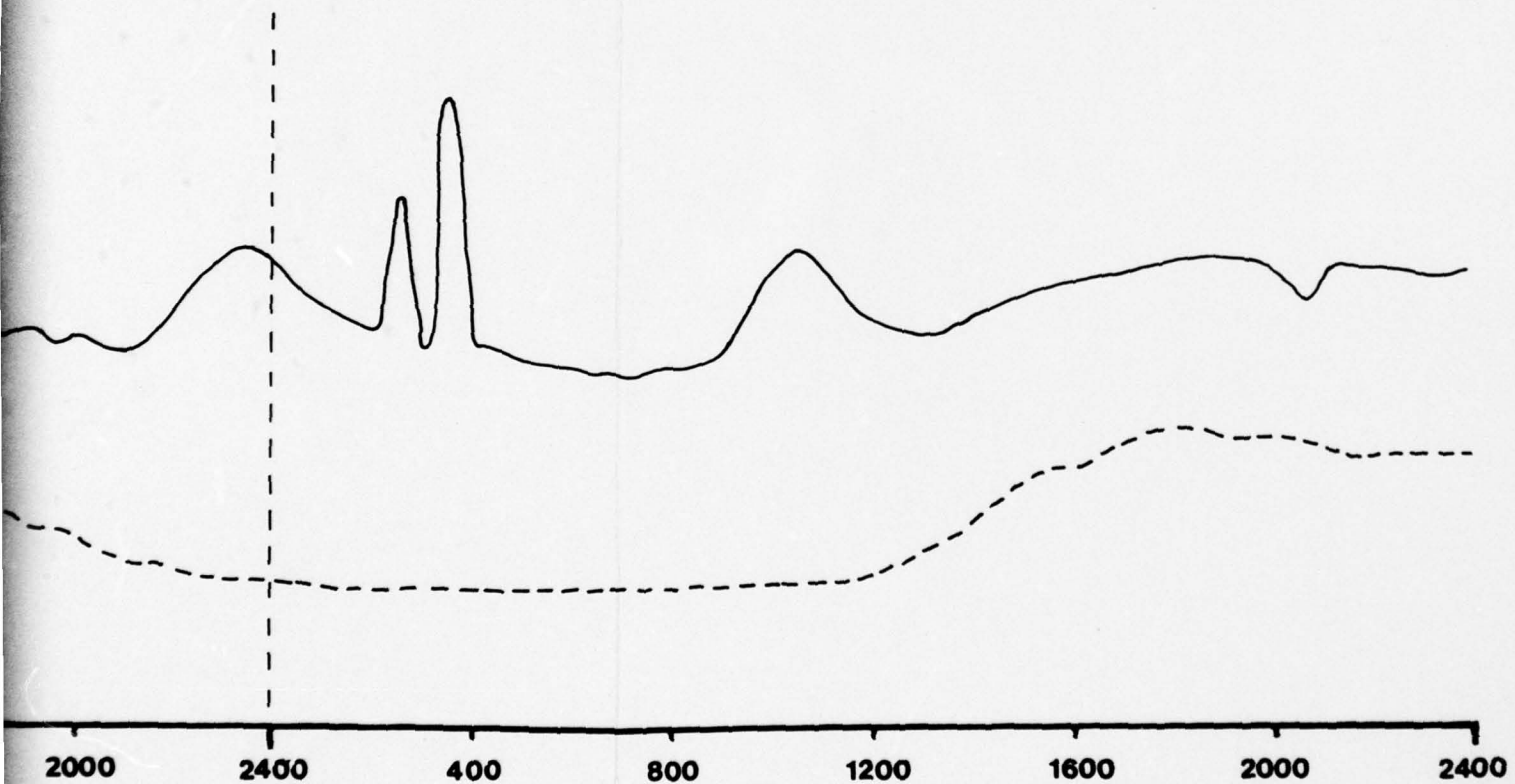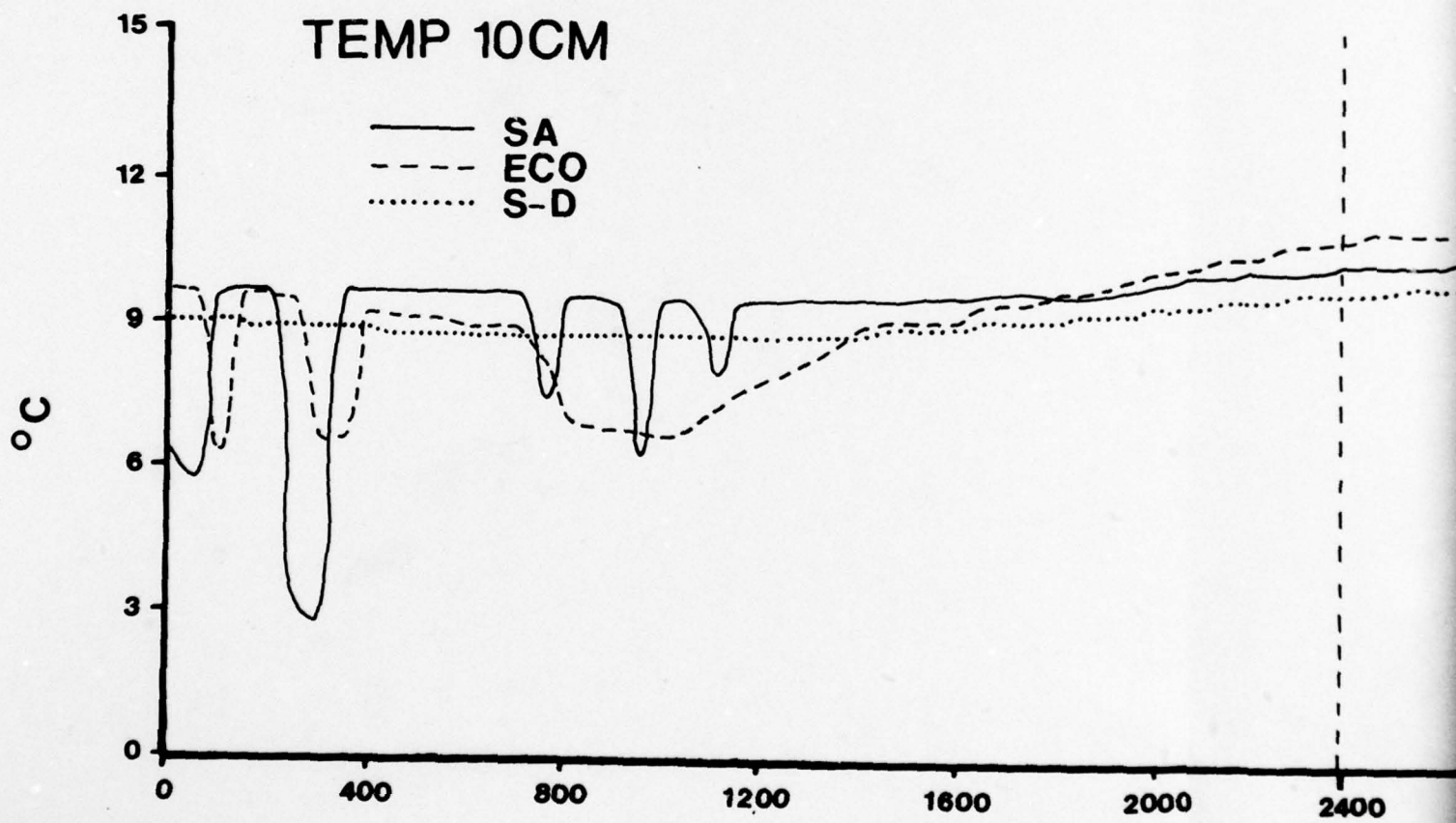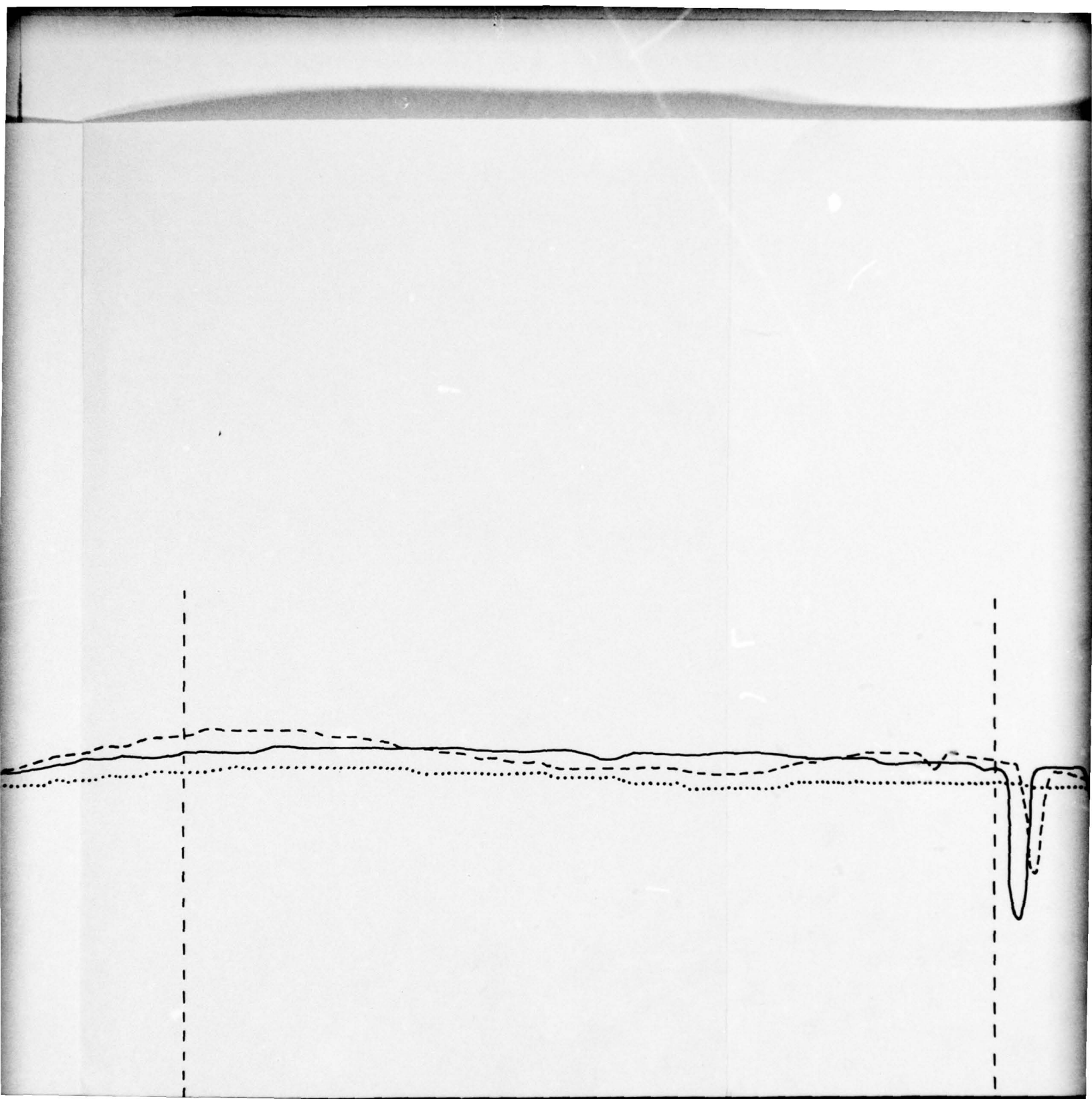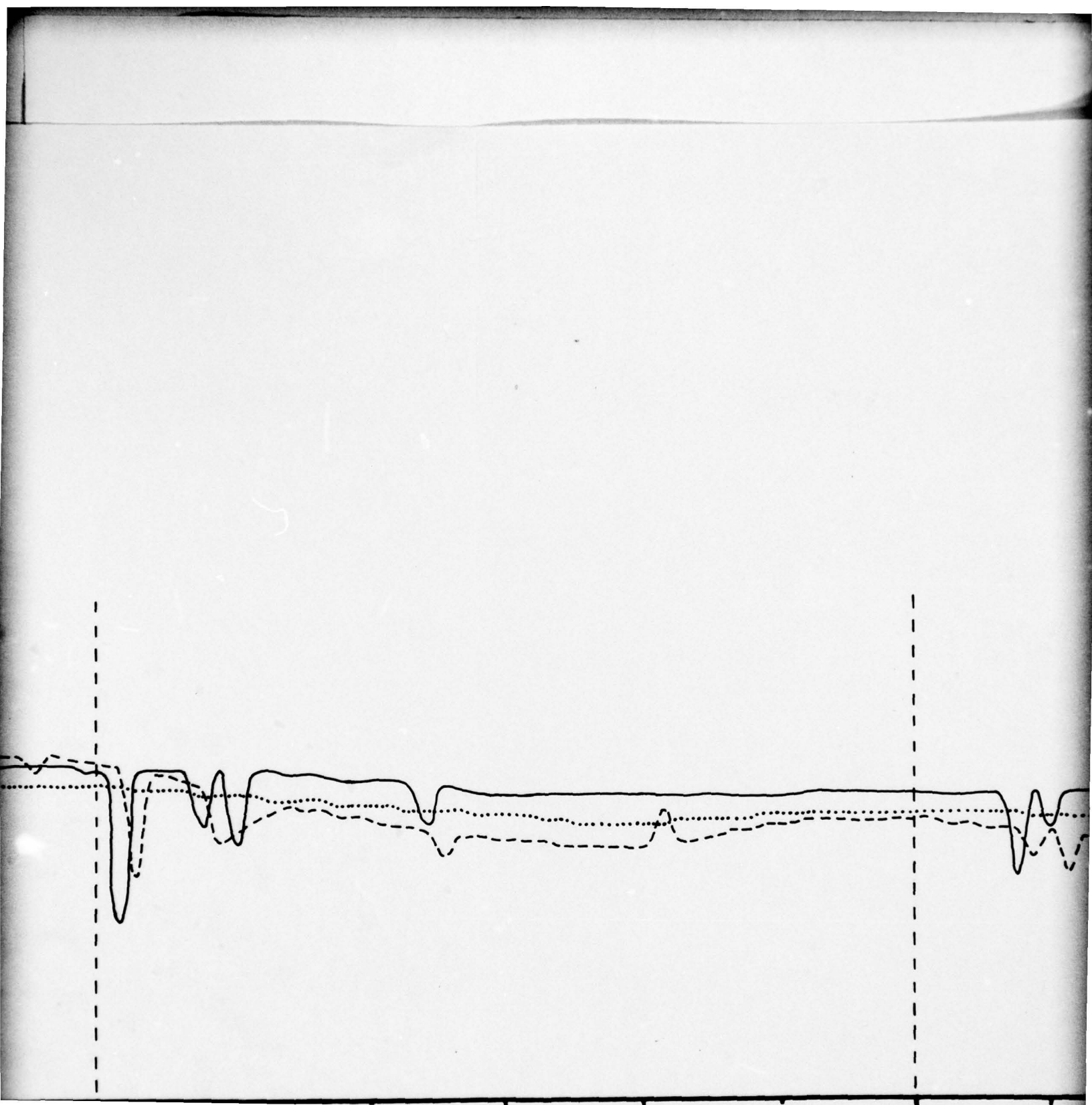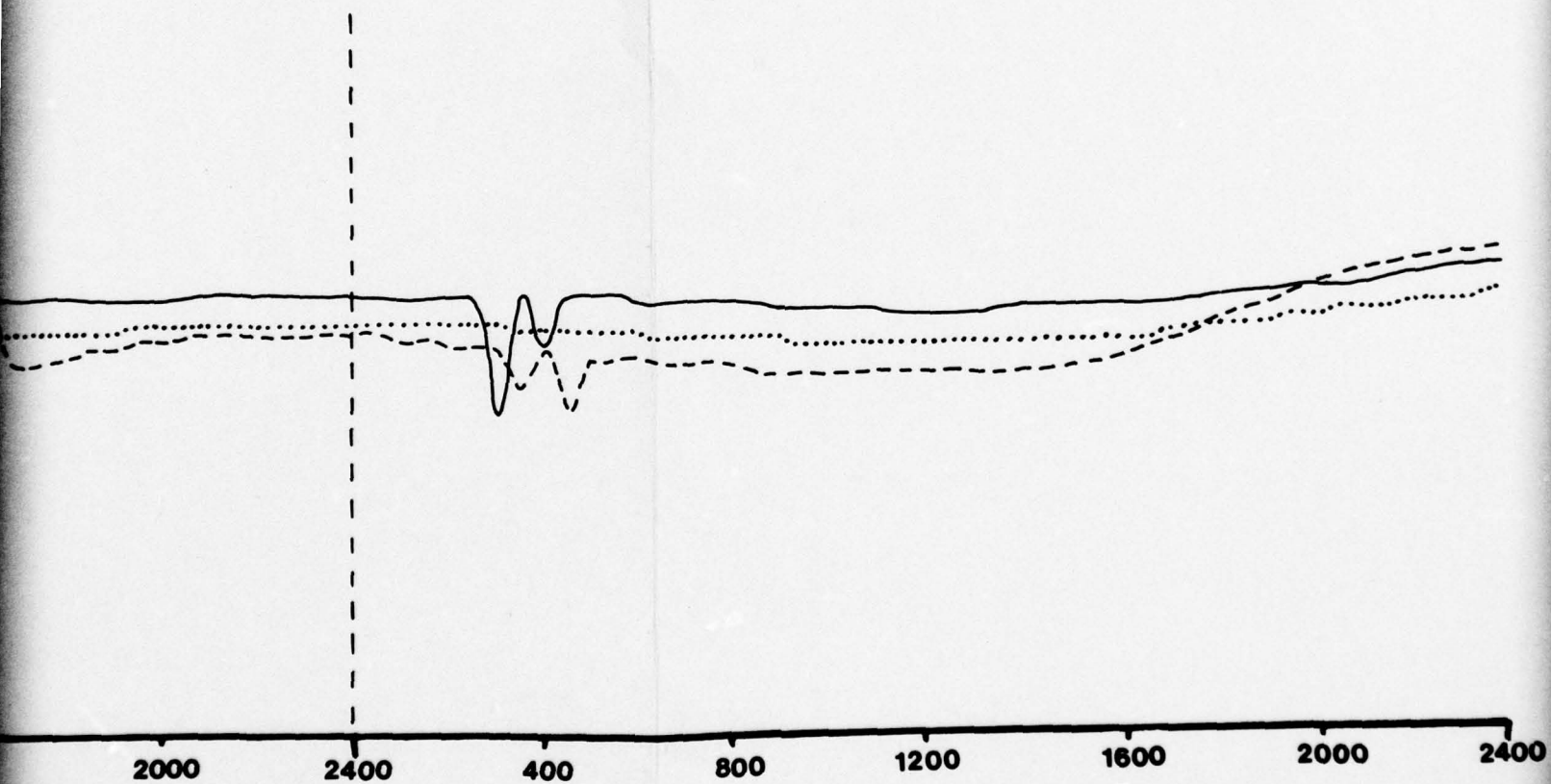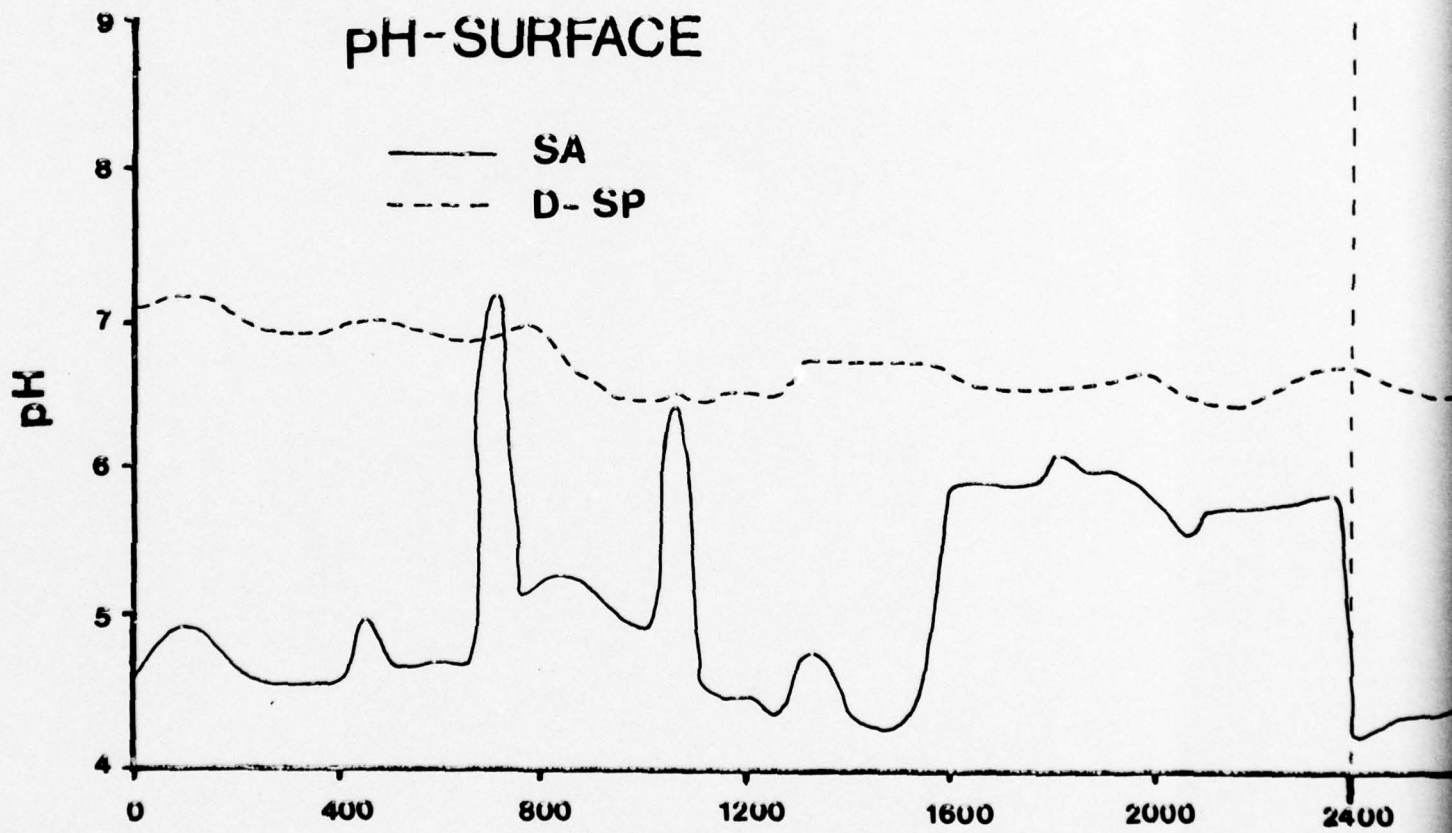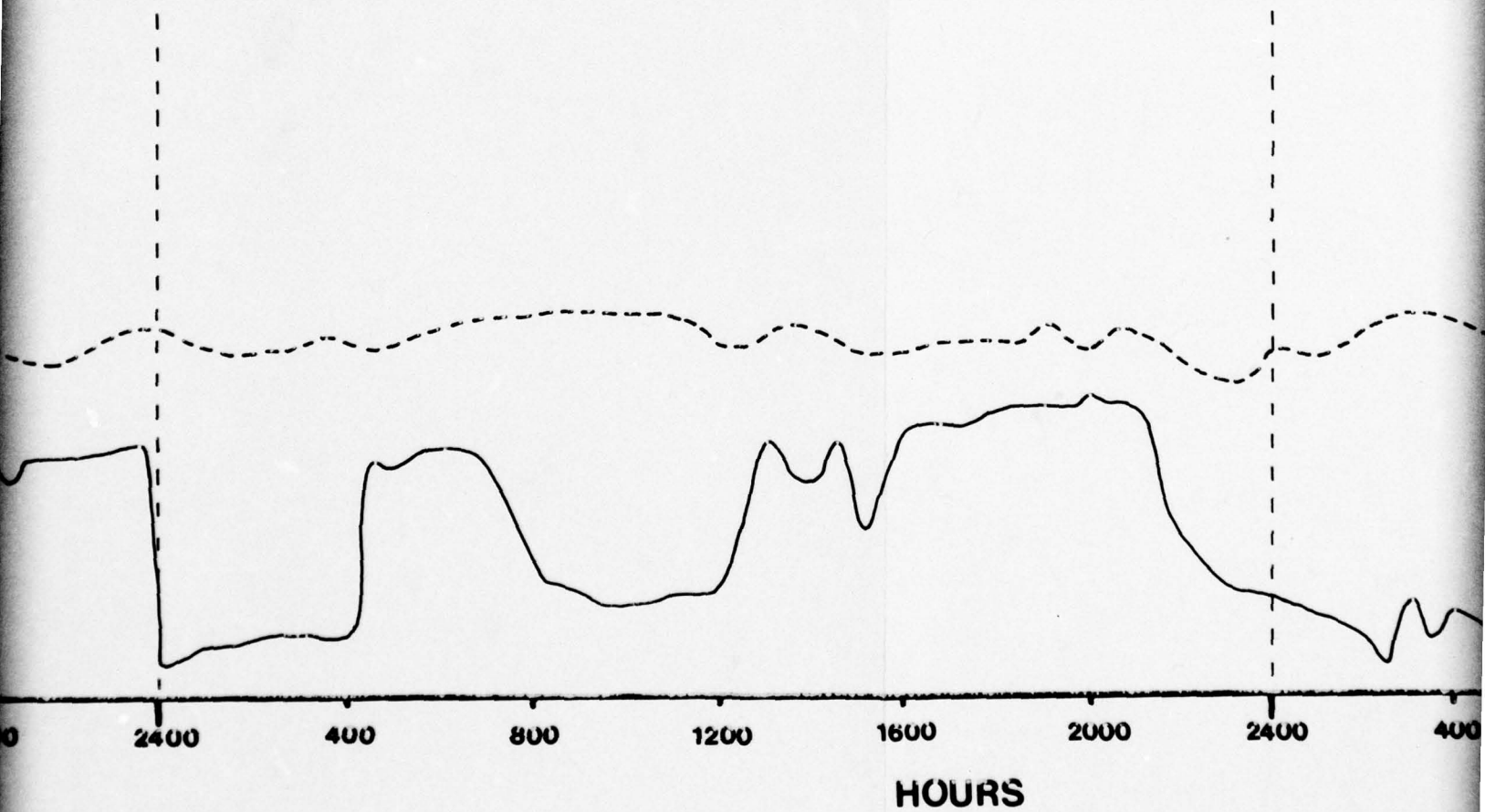
pH-SURFACE

Figure 29. pH at the sediment surface at Taskinas Marsh from

HOURS

ce at Taskinas Marsh from 25 to 28 November 1975.

2400 400 800 1200 1600 2000 2400 400

2000   2400   400   800   1200   1600   2000   2400

4

pH 10CM

SA
ECO
D-SP
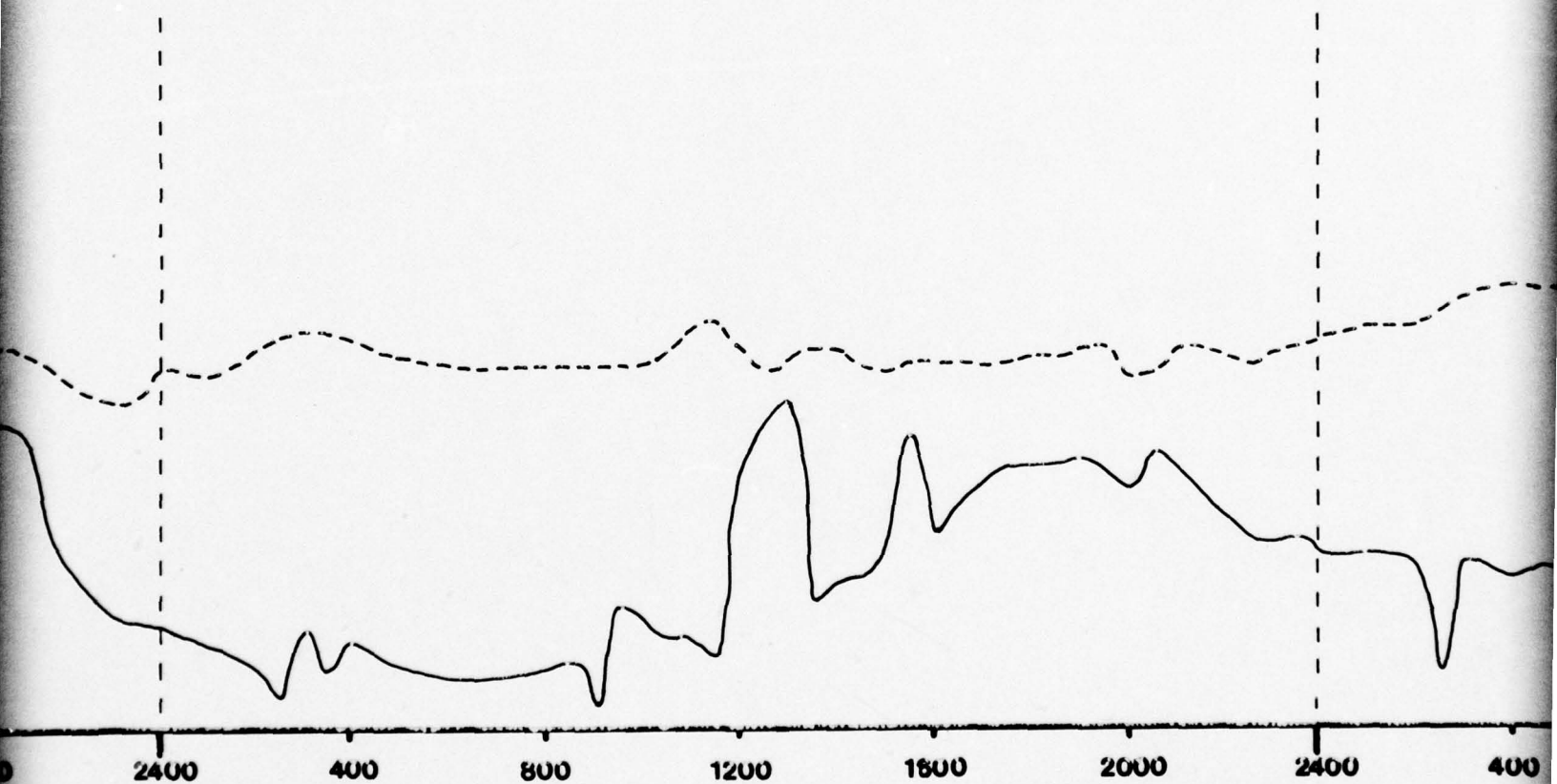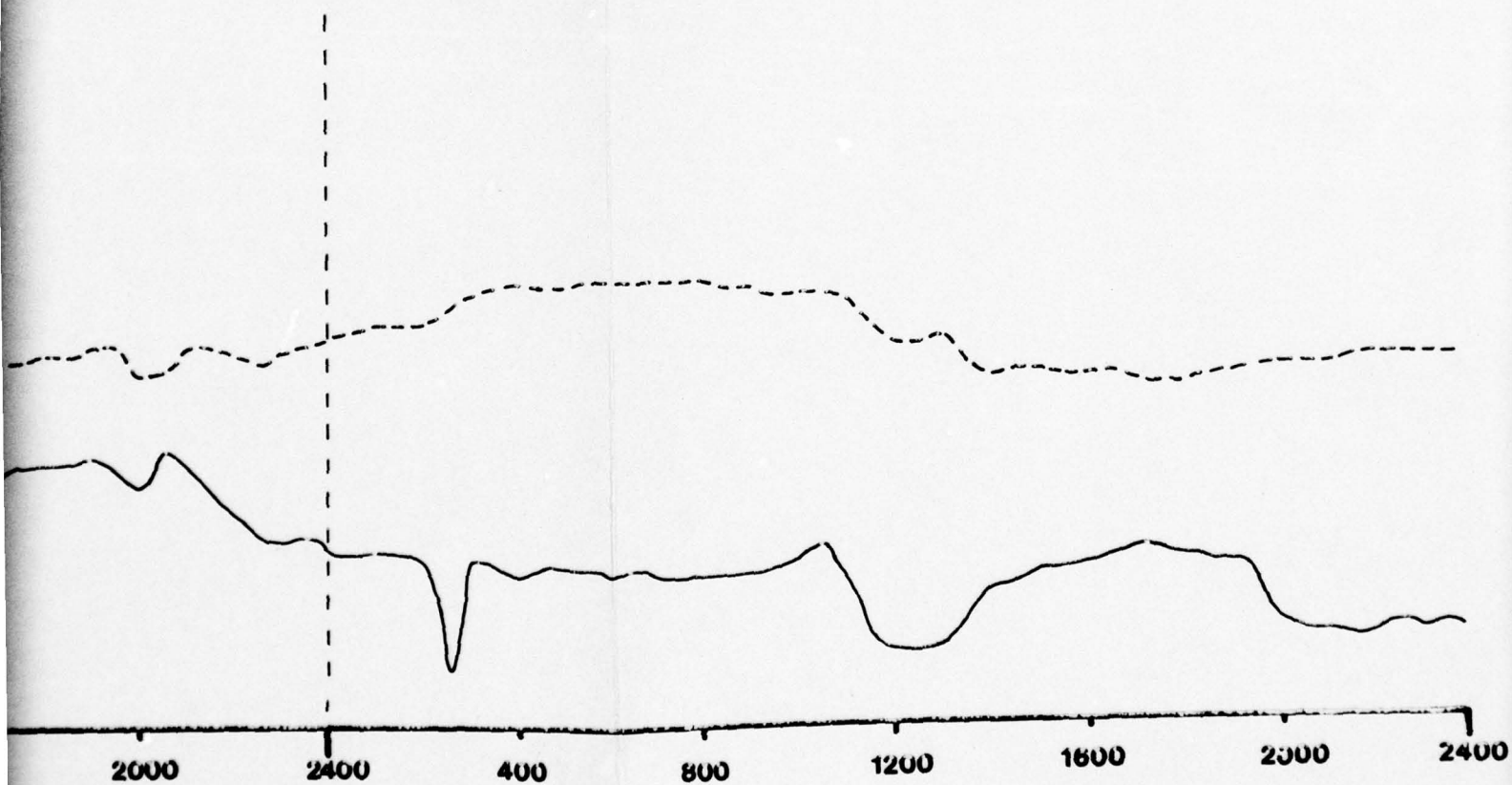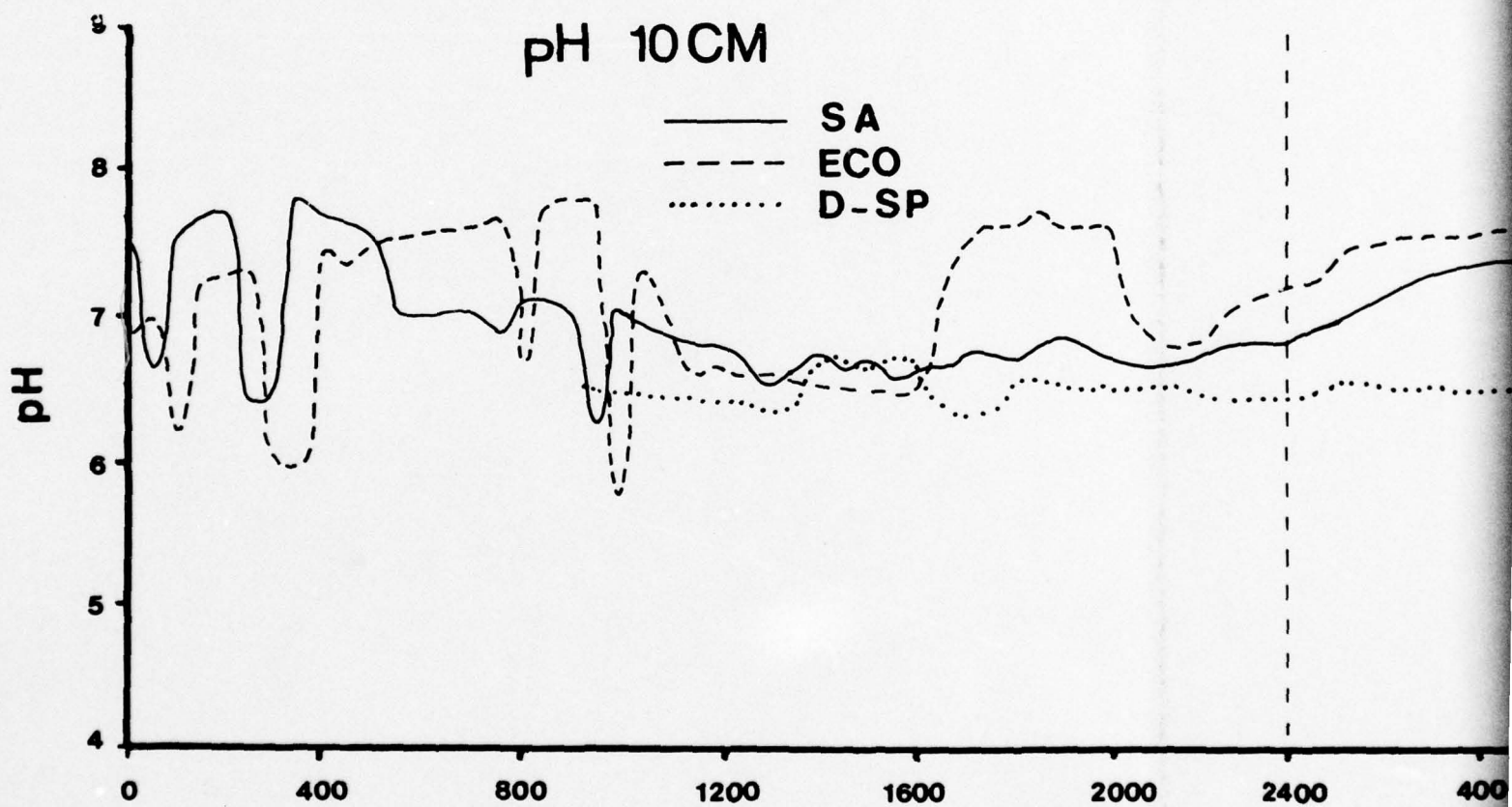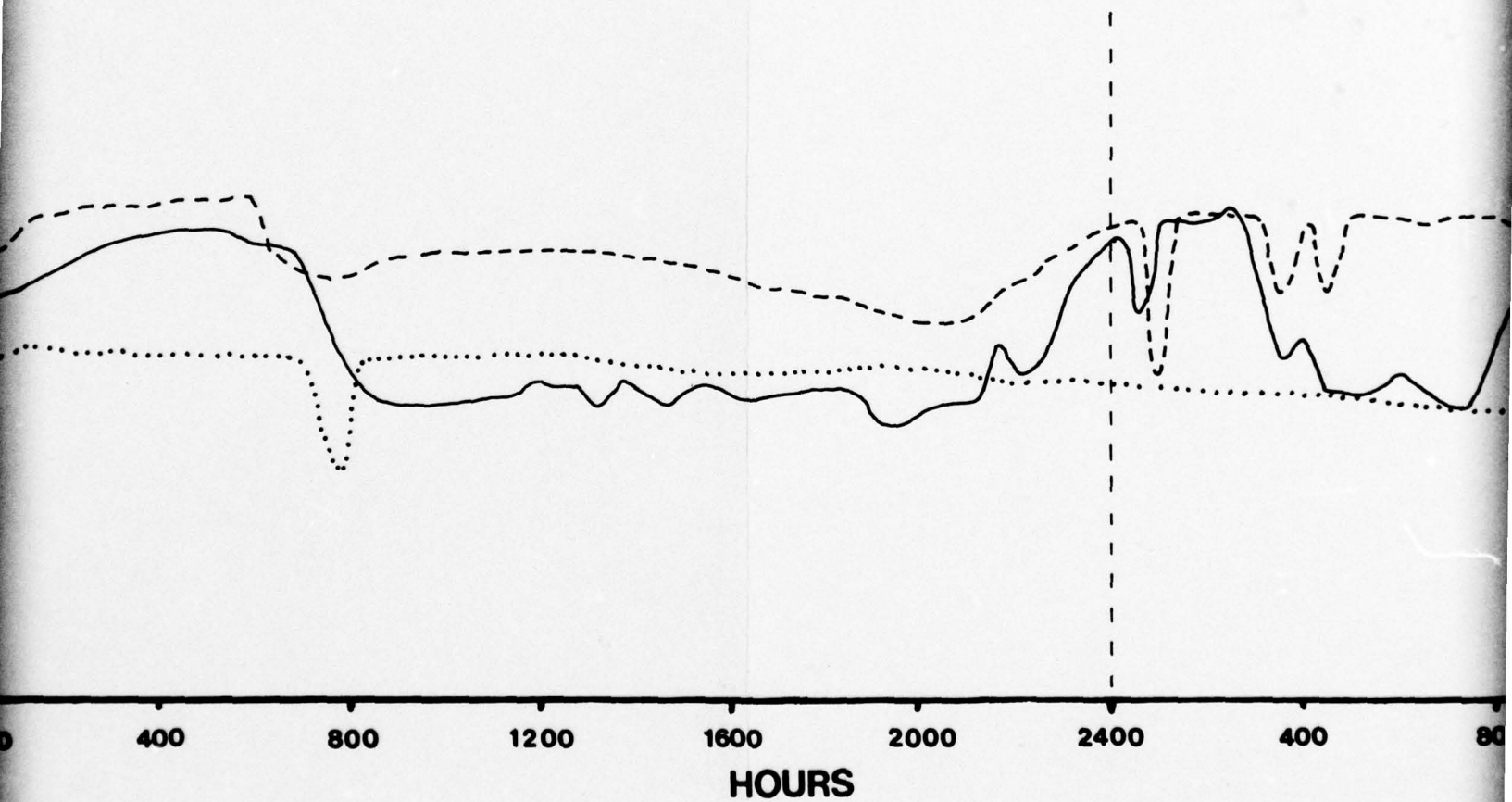
Figure 30. pH at 10 cm in the sediment at Taskinas Marsh from 25 to 28 No

400   400   800   1200   1600   2000   2400   400

askinas Marsh from 25 to 28 November 1975.

2000   2400   400   800   1200   1600   2000   2400
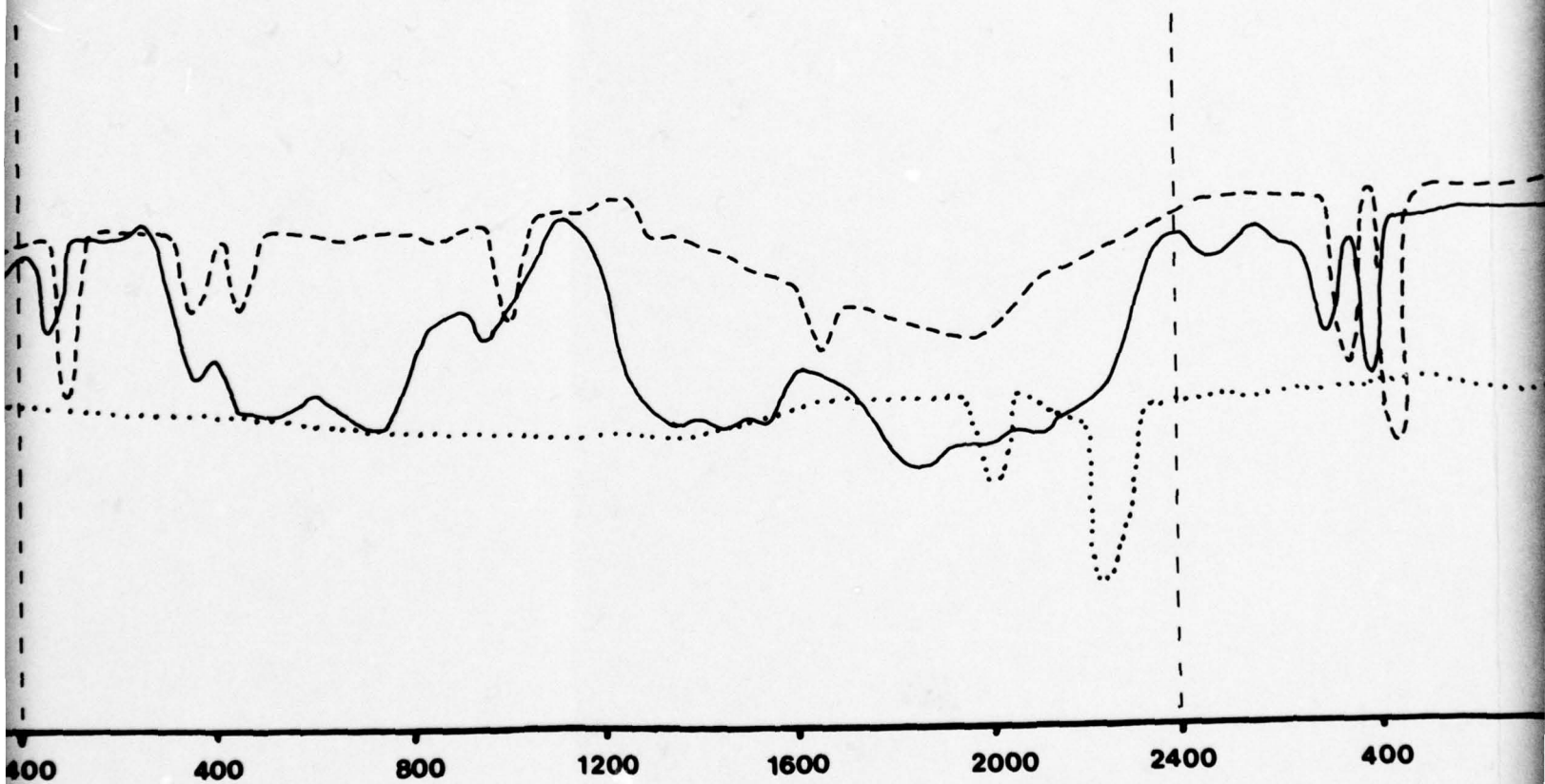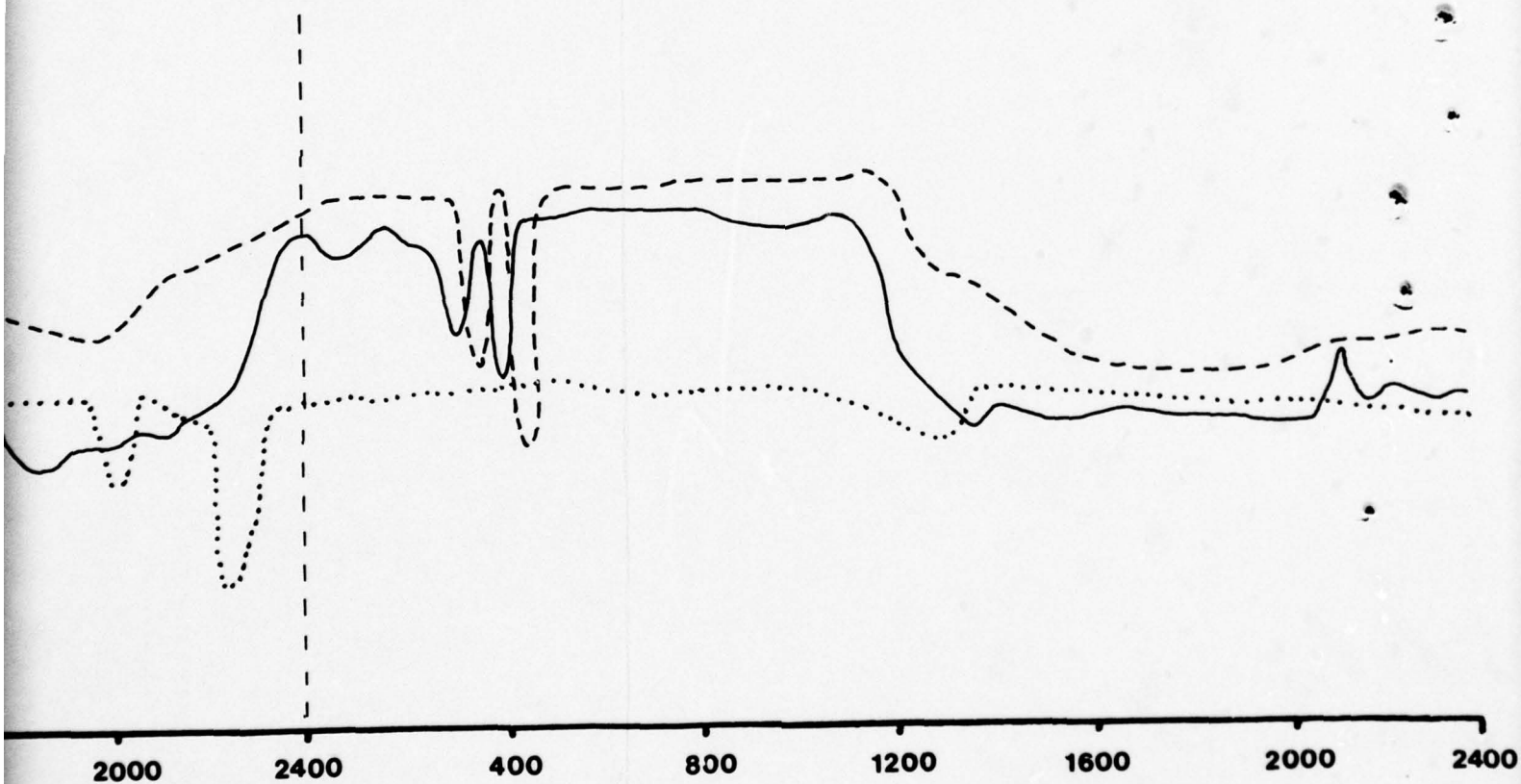
4

102. Because the data were continuous and spanned several cycles of the driving function, they could be analyzed by rigorous mathematical techniques, including Fourier series analysis (Rayner, 1971; Platt and Denman, 1975). This technique is utilized to determine if an environmental forcing function such as tide or radiation exerts an effect on another parameter. Alternatively, it can be used to reduce large amounts of data, such as the voluminous time series records collected here. A Fourier series is a composite of sines and cosines that represent the decomposition of a time series. In this sense it is a form of curve fitting, because the sum of a set of sines and cosines results in the replication of the original curve $\tilde{S}(t)$, where:

$$\tilde{S}(t) = a_0 + \sum_{i=1}^{j-1} a_i \sin(2\pi f_i \Delta t) + b_i \cos(2\pi f_i \Delta t)$$

$\tilde{S}(t)$ = approximation of original time series

a_0, a_i, b_i = Fourier coefficients

$f_i = i^{th}$ harmonic of fundamental frequency

Δt = data sample time interval

The coefficients a_0, a_i, and b_i are Fourier coefficients and reflect the influence of each sine and cosine component in the reconstitution of the original information.

103. For example, if the original time series $\tilde{S}(t)$ is a tidal record with zero amplitude at time zero (t_0), the Fourier series representation of this curve would be

$$\tilde{S}(t) = a_i \sin(2\pi f_i \Delta t)$$

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where $\sin(2\pi t/T)$ represents a frequency of 2 cycles/day. All of the

other frequencies would have very small coefficients associated with

them since tides in the Virginia area are nearly sinusoidal, with a pri-

mary frequency of 2 cycles/day (U.S. Dept. of Commerce, 1974). The

above information is often displayed in graphical format resulting in

what is called a power spectrum. This graph depicts the relationship

between frequency and power. The term power signifies the importance of

a particular frequency in reconstituting the original data and is a

function of the Fourier coefficients. Thus, for a tidal curve, a power

spectrum would be composed of a single spike at a frequency of 2 cycles/

day (Figure 31), all other frequencies having very little power.

104. In many cases the power spectrum for a time series is

dwarfed by a spike at zero frequency. When this occurs it is often

difficult to determine if any other frequencies occur as a significant

component of the original data. The zero frequency represents the mean

of the data series, and a filtering procedure is often utilized to elim-

inate such low frequencies. Following this filtering, it can be ascer-

tained whether the ecologically important frequencies such as 1 and 2

cycles/day are present in the time series under study. For example,

consider a pH time series for surficial sediment in a salt marsh. The

pH may vary around a mean of approximately 5 to 7 pH. To analyze this

time series for frequencies in the range of 1 to 2 cycles/24 hours, the

mean must be removed from the data. This is often accomplished by util-

izing a differencing filter, or simply by subtracting the mean of the

data set from each individual data point. In the case of the differ-

encing filter the data point of a time series at time t is subtracted

104
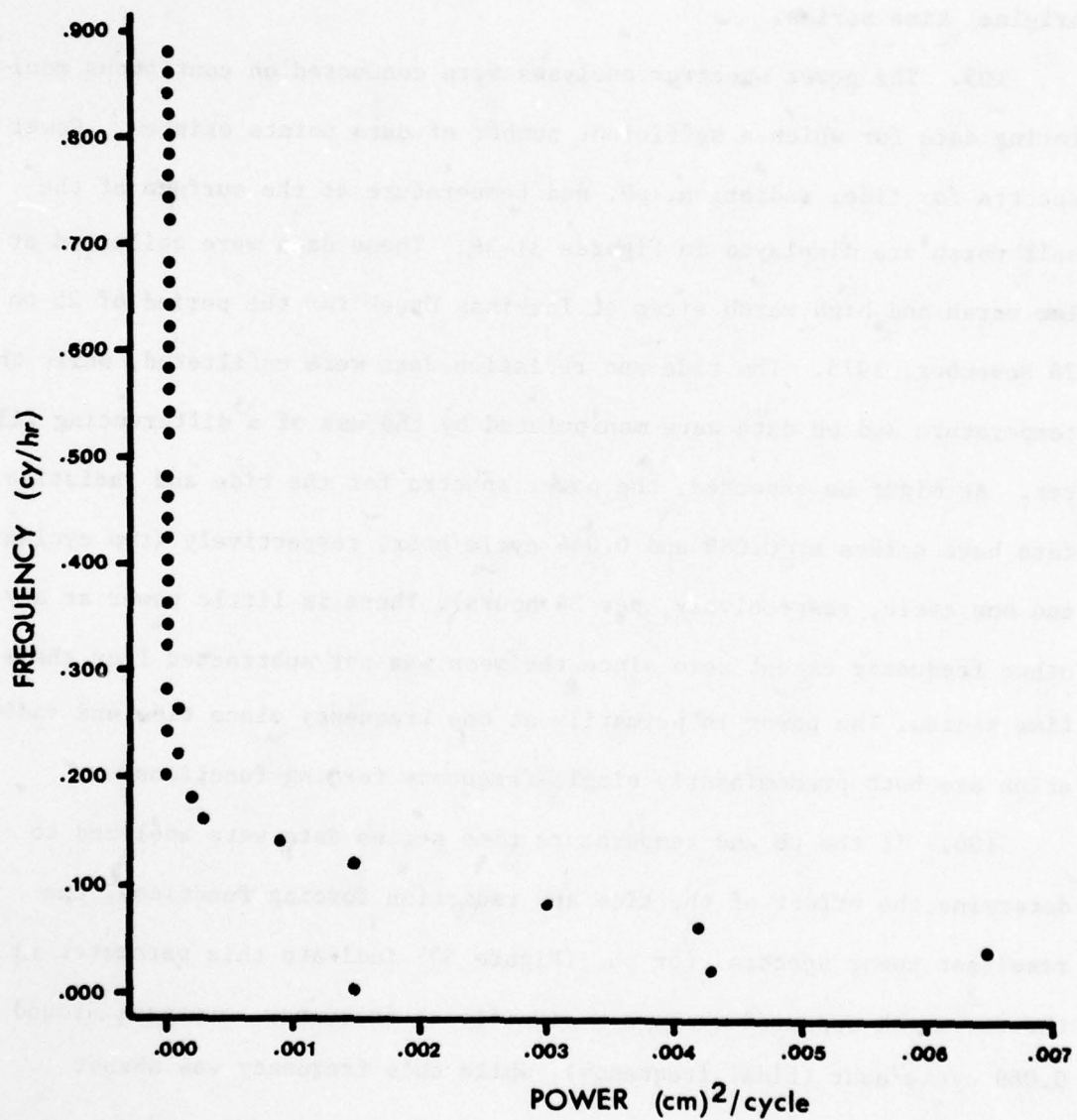
Figure 31.   Power spectrum of tide at Taskinas Marsh.

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from the data point at time t+1, thus constituting a new value at time

t. The process is continued for the entire time series. The result of

this mathematical manipulation is the loss of low frequencies from the

original time series.

105. The power spectrum analyses were conducted on continuous moni-

toring data for which a sufficient number of data points existed. Power

spectra for tide, radiation, pH, and temperature at the surface of the

salt marsh are displayed in Figures 31-36. These data were collected at

low marsh and high marsh sites at Taskinas Creek for the period of 25 to

28 November, 1975. The tide and radiation data were unfiltered, while the

temperature and pH data were manipulated by the use of a differencing fil-

ter. As might be expected, the power spectra for the tide and radiation

data have spikes at 0.089 and 0.044 cycle/hour, respectively (two cycles

and one cycle, respectively, per 24 hours). There is little power at any

other frequency except zero since the mean was not subtracted from these

time series. The power is primarily at one frequency since tide and radi-

ation are both predominantly single-frequency forcing functions.

106. If the pH and temperature time series data were analyzed to

determine the effect of the tide and radiation forcing functions, the

resultant power spectra for pH (Figure 33) indicate this parameter in

the low marsh appeared to have a significant frequency component around

0.089 cycle/hour (tidal frequency), while this frequency was absent

in the high marsh pH data. The surficial temperature data also

reflect the tidal influence elucidated above. As is seen in Figure 34,

the temperature power spectrum for low marsh had a large spike at the

tidal frequency of 0.089 cycle/hour. The temperature time-series data

106
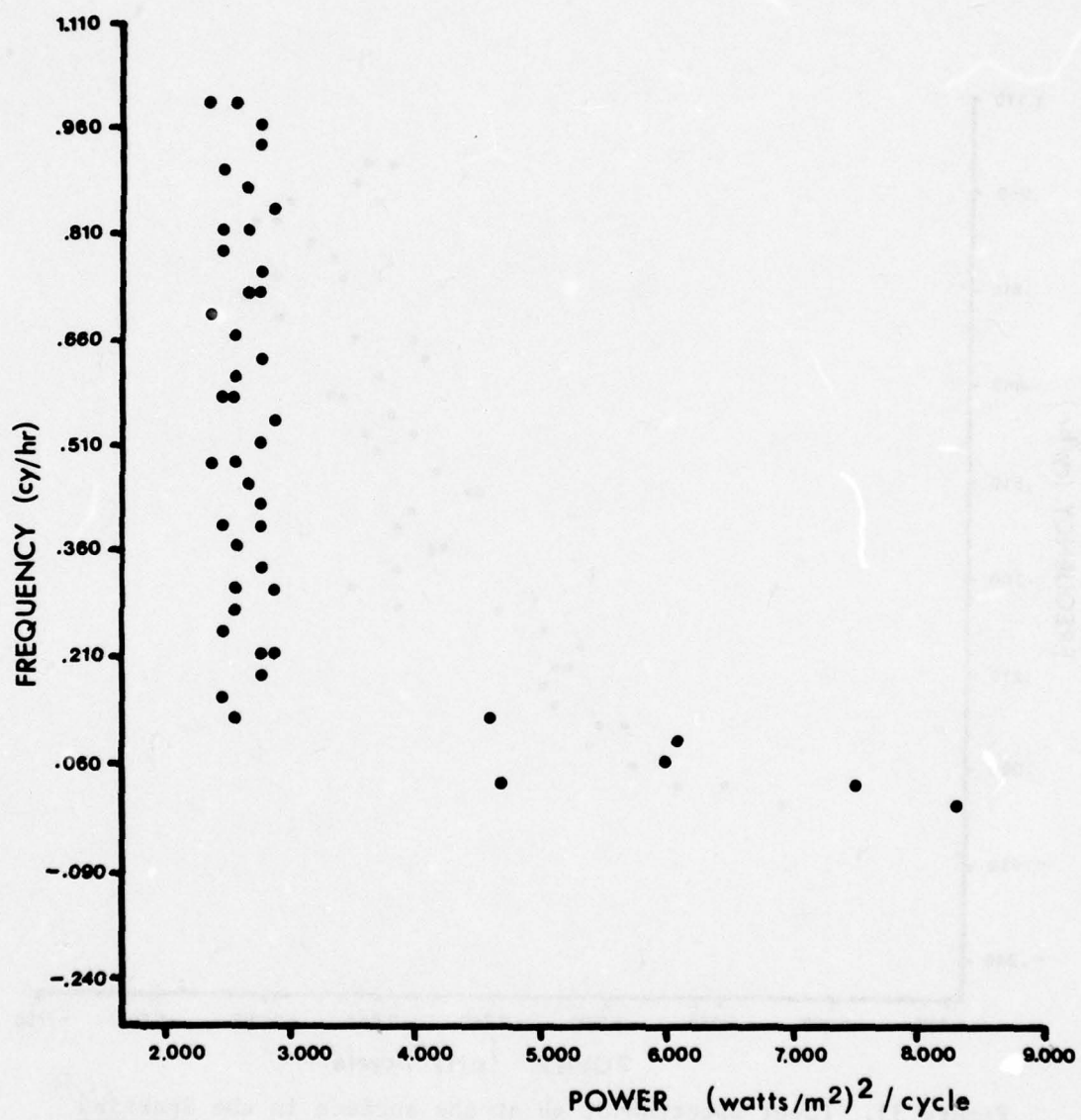
Figure 32. Power spectrum of solar radiation at Taskinas Marsh.

107
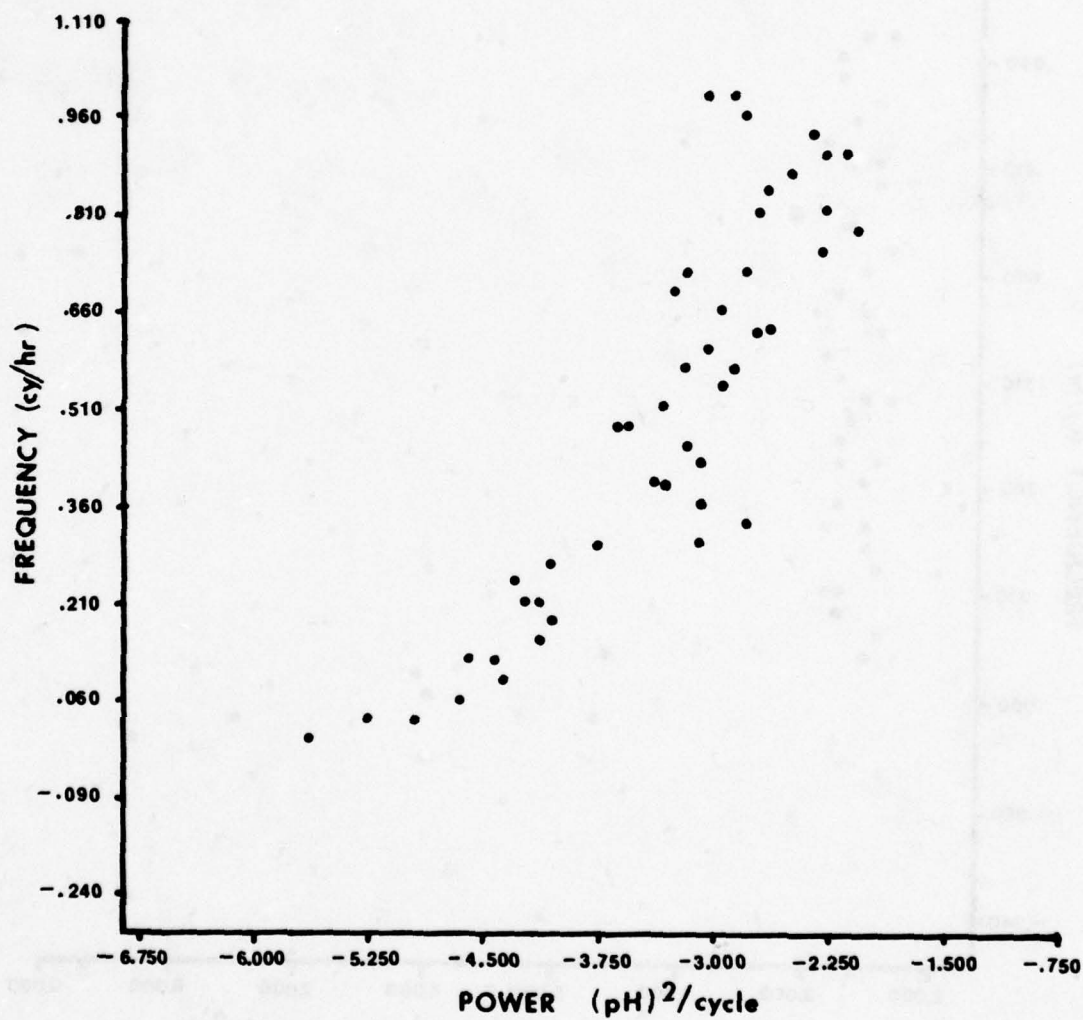
Figure 33. Power spectrum of pH at the surface in the _Spartina alterniflora_ zone at Taskinas Marsh.
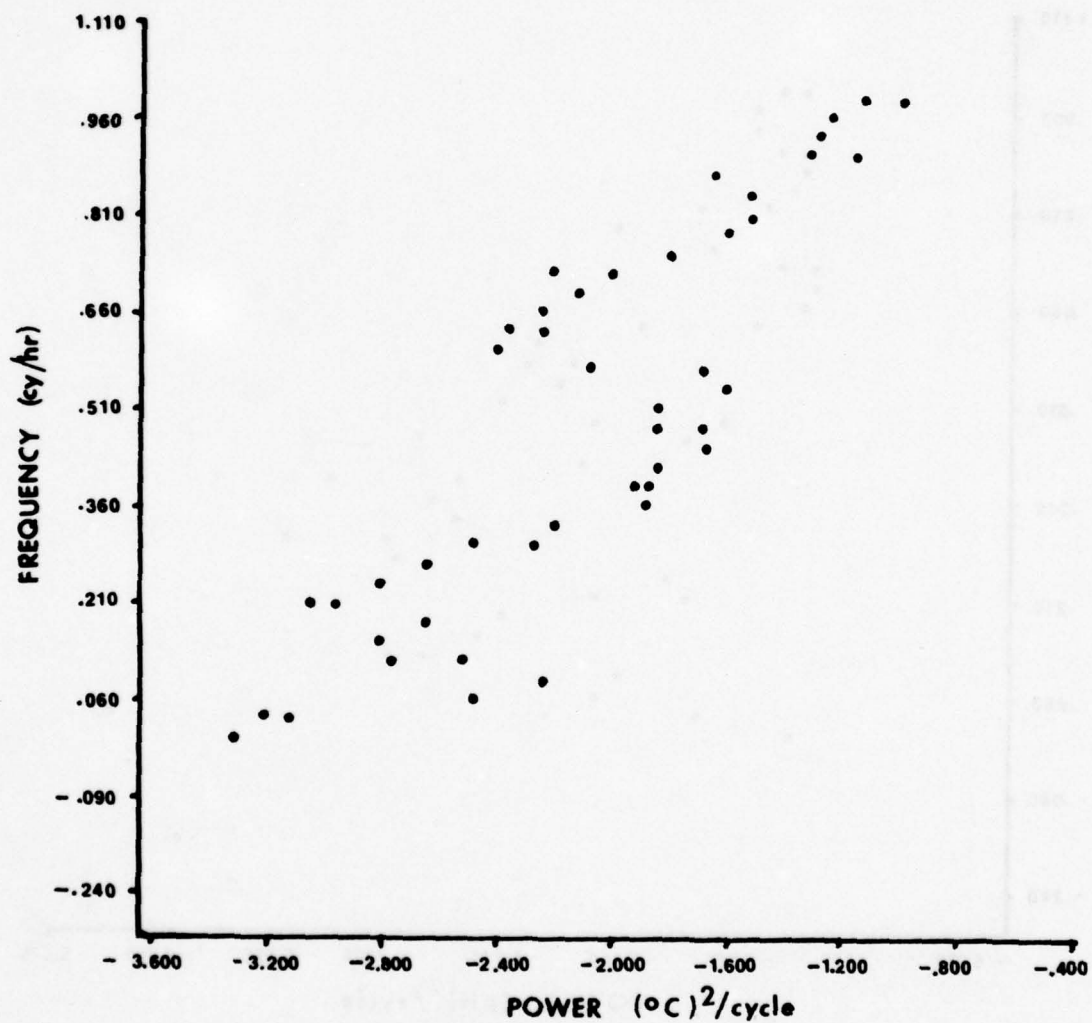
Figure 34. Power spectrum of temperature at the surface in the _Spartina alterniflora_ zone at Taskinas Marsh.

Figure 35. Power spectrum of pH at the surface in the _Spartina patens – Distichlis spicata_ zone at Taskinas Marsh.
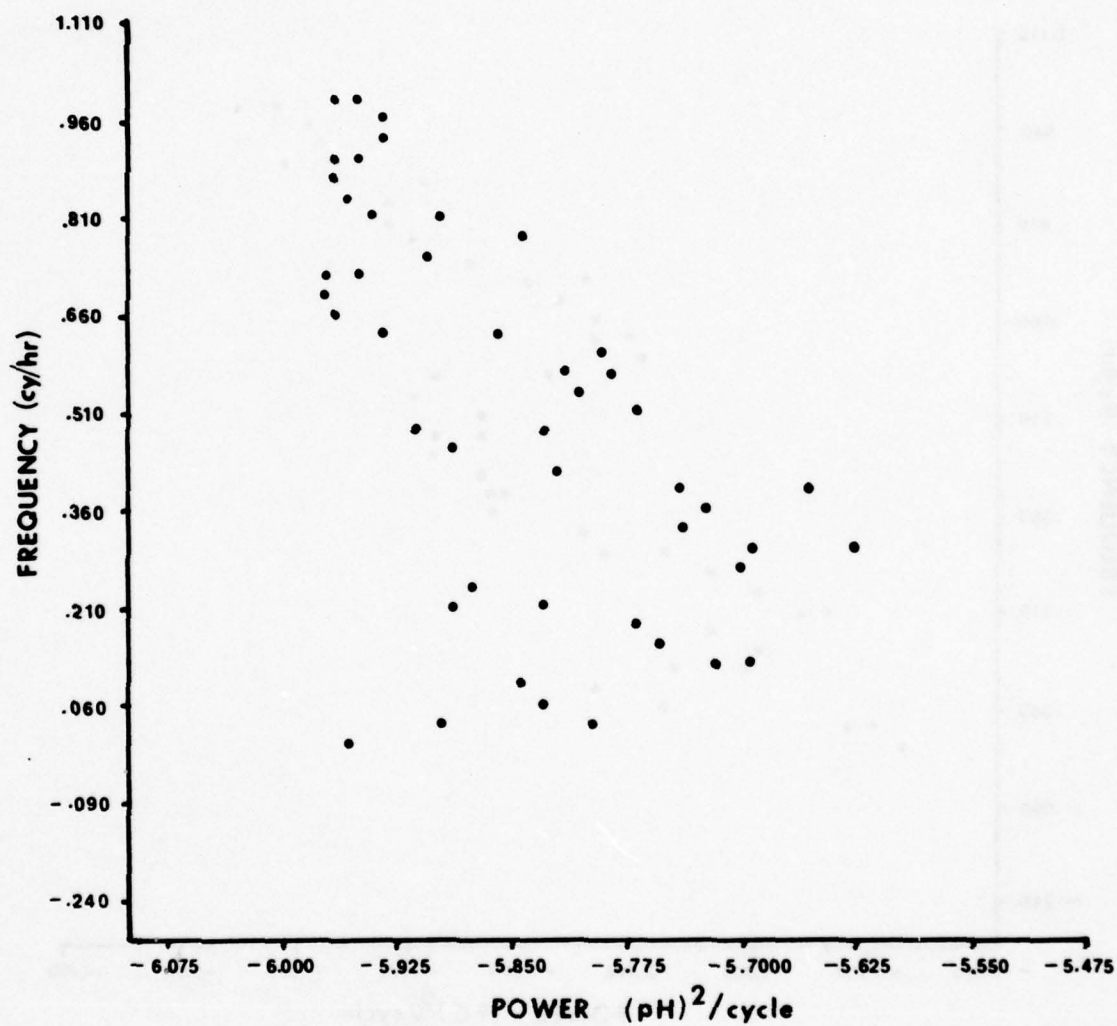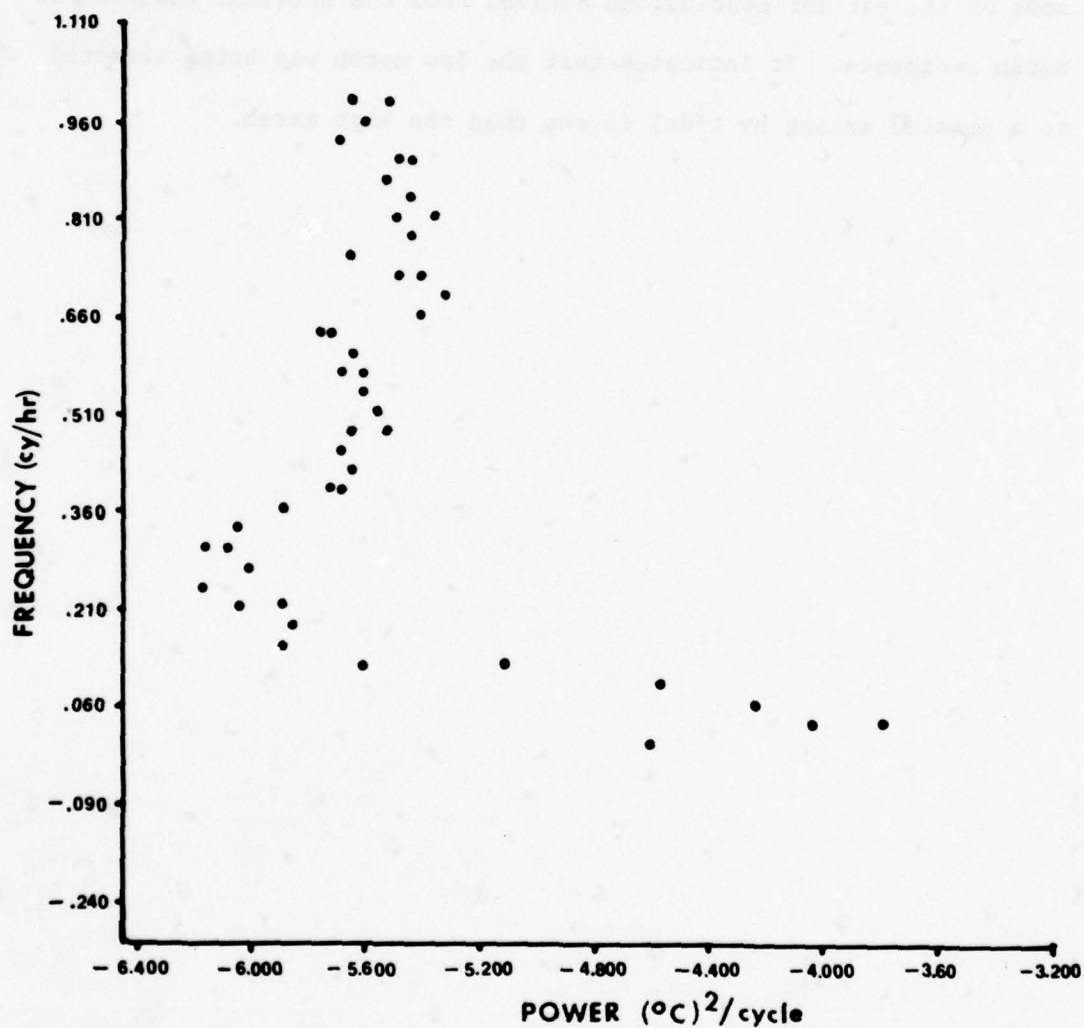
Figure 36. Power spectrum of temperature at the surface in <u>Spartina</u> <u>patens</u>- <u>Distichlis</u> <u>spicata</u> zone at Taskinas Marsh.

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for the high marsh lacked the tidal frequency but had a large frequency component near 1 cycle/day, which was the primary radiation frequency.

107. This analysis supplements, and to a degree substantiates, some of the earlier conclusions derived from the nutrient analysis of marsh sediments. It indicates that the low marsh was being affected to a greater extent by tidal forces than the high marsh.

PART VII: MARSH SUCCESSION MODEL

108. One of the major objectives of this project was to develop
a model to simulate the growth and succession of major plant species
on natural marshes and on dredged material disposal sites. Accordingly,
model development paralleled the field phase of the project. To pro-
duce a simulation model of plant growth and succession on salt marshes,
several modeling approaches may be taken. The ideal approach is to
work from a complete understanding of the underlying ecological prin-
ciples that cause the growth and death of plants. This yields a model
that can accurately depict the response of a plant to the environ-
mental factors--physical, chemical, and biological--that influence the
study species. However, the biology of most organisms is insuffi-
ciently understood to develop models at this level of resolution. The
other extreme in model design is a model whose linkages are totally
empirical. Such a device is usually developed to test the accuracy of
predicting outputs from a series of chosen inputs, with little atten-
tion given to the realism of the model's internal processes. Super-
ficially, this type of model seems ideal for many purposes. However,
as any type of model is produced, it is inevitably necessary to make
some simplifying assumptions ; and in the case of the highly empirical
model, the assumptions may severely limit the usefulness of the final
product.

109. Early experimental models produced for this study were
highly realistic growth models based primarily on studies involving
Spartina _alterniflora_. However, their extreme complexity made them

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difficult to use. One of the major concerns in this project was that the final model should be easily manipulable for individuals with only a basic understanding of the use of computers; it was therefore judged that the highly realistic models, which demand thorough acquaintance with both computer science and salt marsh ecology, were unsuitable.

110. The inherent complexity of the initial models also emphasized another problem that aided in the development of the present model. Like any complex mechanical device, a model is limited by its weakest components (consequently constructing a model that is complex in some of its functions but crude in others can often be futile exercise). The marsh literature, though extensive, is largely descriptive in nature, and little information is sufficiently quantitative to be applied toward development of a simulation model. Spartina alterniflora has been studied extensively, yet there are sufficiently large uncertainties about the physiological ecology of this plant that constructing a realistic growth model is difficult. Knowledge of the physiology and ecology of S. patens and D. spicata is even more limited. Thus, in constructing a realistic model using these three species, one must make a choice: either be constrained by the species for which the least information is available, or make assumptions about this species' responses based on the behavior of closely related species.

111. Since assumptions must always be made in building a model, constraints must be imposed on the model's use. For instance, if a growth model is developed to simulate the response of a species to several factors within an assumed salinity range of 10 to 35 percent, a

salinity input of 5 percent may produce a response that is seriously misleading.

Model Concept

112. The central units of the succession simulation were submodels of the growth dynamics of each species, called species modules. The original species module developed was for Spartina alterniflora, because there was more information available for this species than for other salt marsh plants. A frequent drawback of simulation models developed with scarce data was their inability to evolve as the data base increased. The species modules were developed to be open-ended; that is, as more information became available documenting the response of the plants to environmental factors, it could be used to increase the realism of the module.

113. The same basic species module structure, considered to be representative of a generalized salt marsh plant, was used for all species (Figure 37). The differing responses of the individual species were incorporated by imbedding response curves within each module to characterize the response of given species to selected environmental variables.

114. The model described here utilized three species modules, representing S. alterniflora, S. patens, and D. spicata, but possessed the capability of utilizing up to 10 species modules whether they were used to represent individual species or functional groups of species.

115. The species modules were combined into a point model that
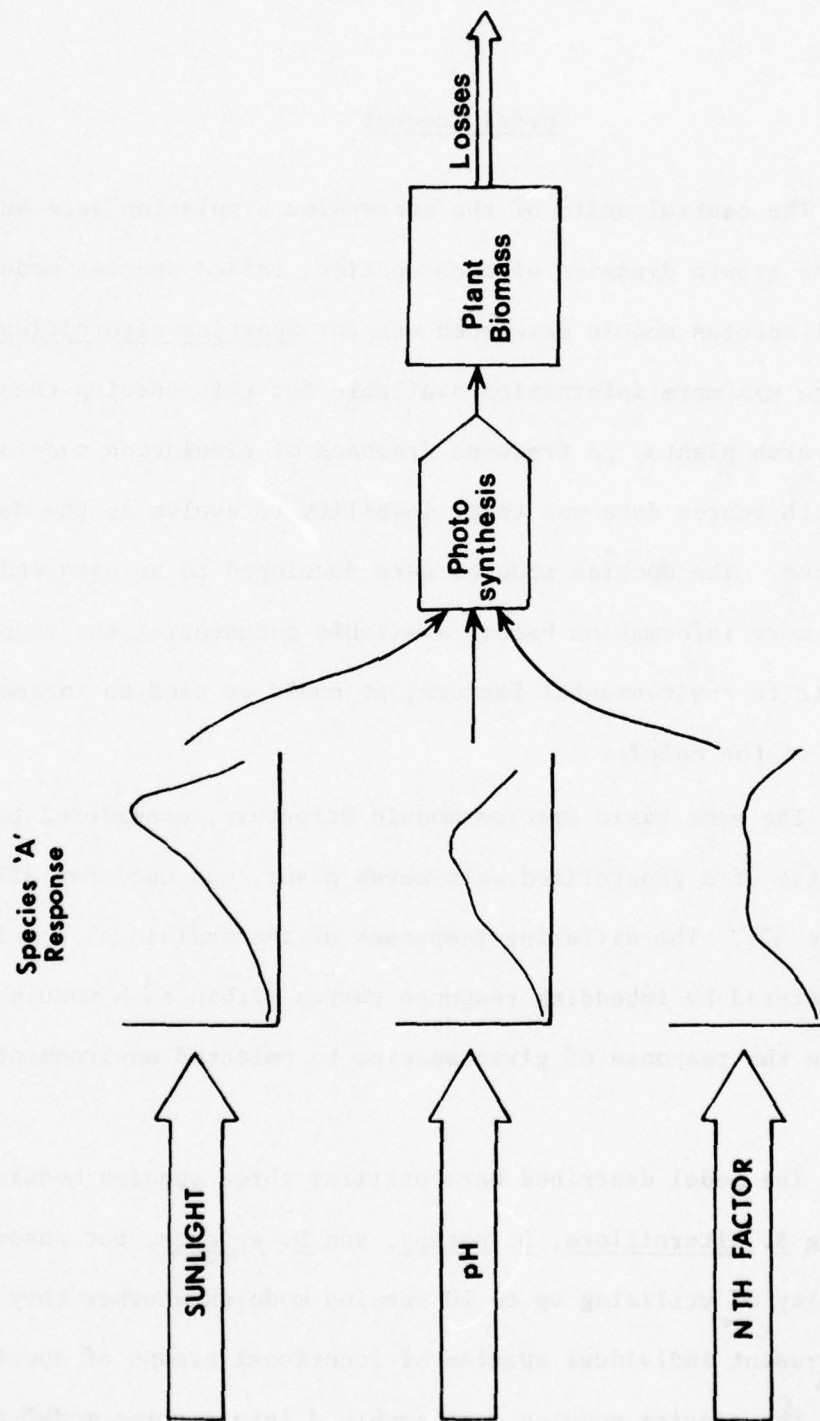
Figure 37. Conceptual diagram of a single species module. The curves represent a generalized response of the plant (y-axis) and the level of the driving variable (x-axis).

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simulates the growth of each species on a particular square meter of marsh surface (Figure 38). Because each point model contains all species modules, it can simulate the growth of co-occurring species at a particular point in the marsh through time. The current model can depict plant growth and succession on a transect across a salt marsh by using physical variables to link series of point models. Coupling of the point models, each of which represents a discrete point on the marsh surface, enables simulation of plant growth both temporally and spatially (Figure 39) on the marsh from the tidal creek to the high marsh.

116. The current version of the model, MARSH1, contains the three species modules previously described, and is driven by four environmental factors: solar radiation, temperature, soil salinity, and tidal inundation. A wide variety of mathematical formulations are available to describe the growth of the plant using such a set of driving variables. Probably the most common method utilizes a multiplication technique where growth is a result of some factor "A" times a factor "B" times a factor "C" and so on so that the result is a product of a series of driving variables. This is often a very unrealistic way to simulate a response to a series of variables as it assumes interactions among the variables that may be ill-understood or nonexistent.

117. Plant physiologists have clearly established the interaction of temperature and solar radiation in controlling photosynthetic rate. The curves of Gates (1968) depict photosynthesis as a function of various light levels and differing temperatures. However, detailed information is not available for most marsh plants; thus it was felt

117
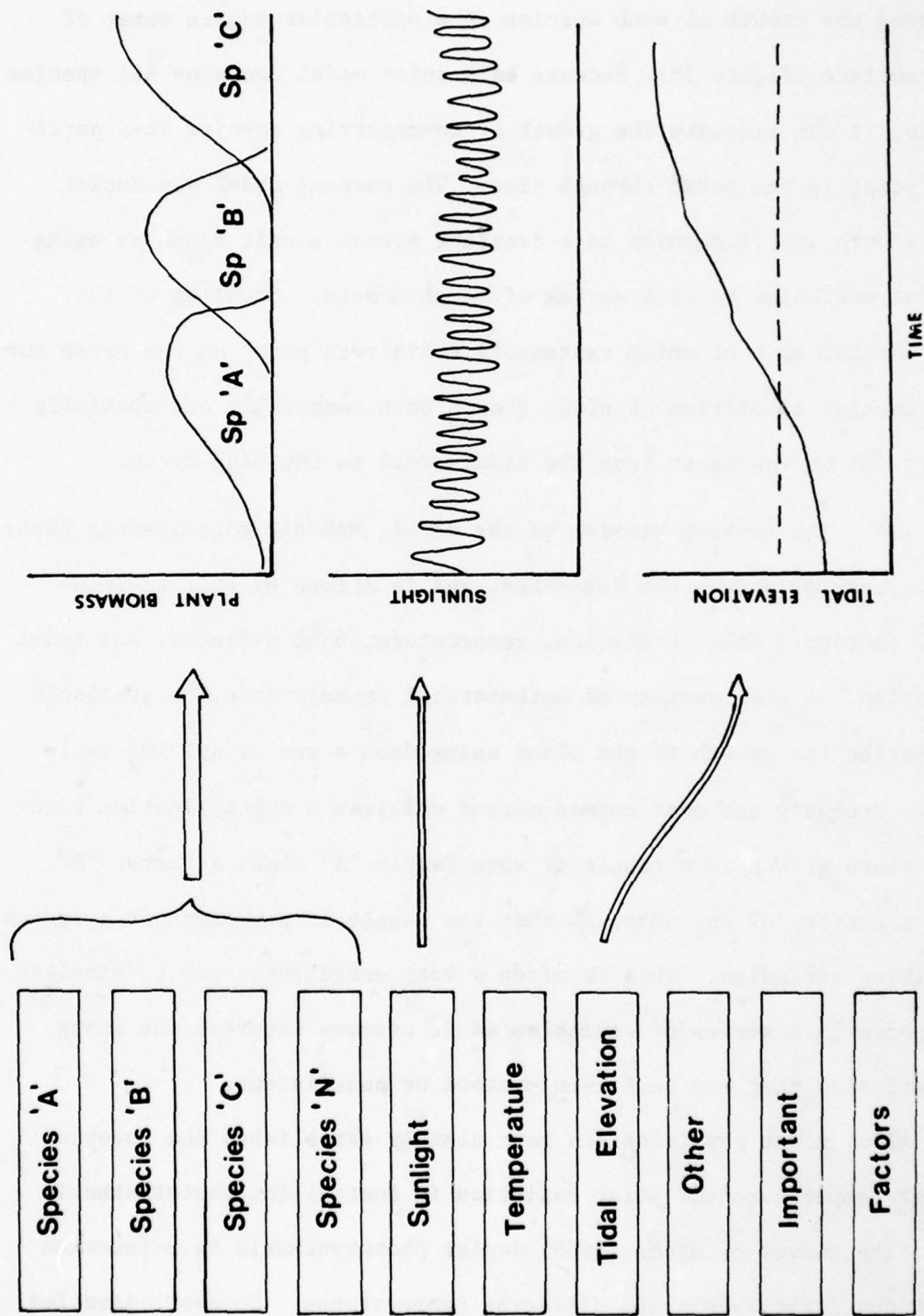
Figure 38. Conceptual diagram of the linking of several species modules with environmental forcing functions to form a model of a single point in the marsh.
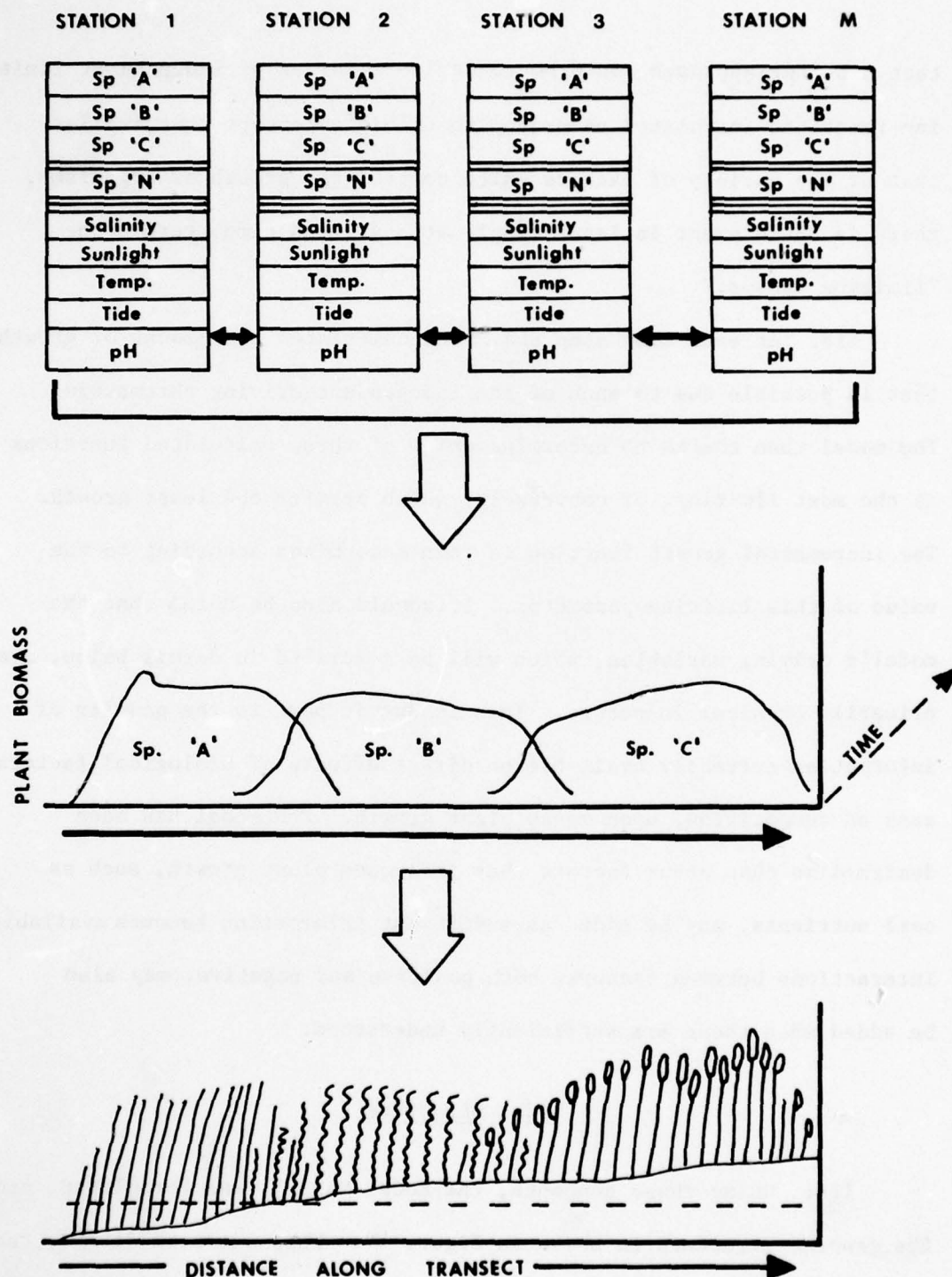
Figure 39. Conceptual diagram showing the coupling of several point models to produce a coupled model of transect with several stations. The middle and lower sections represent generalized plant species distributions on the marsh. The dashed line in the lower section represents mean high water.

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that a better approach would be to devise a series of independent limiting functions formulated according to Liebig's concept that implies that of the variety of factors which control the growth of organisms, there is one element in least supply at any given time, termed the "limiting factor."

118. At each time step the model calculates the amount of growth that is possible due to each of the independent driving parameters. The model then checks to determine which of these calculated functions is the most limiting, or conversely, which permits the least growth. The incremental growth function is then determined according to the value of this limiting parameter. It should also be noted that the model's driving variables, which will be described in detail below, are primarily physical in nature. This is due in part to the paucity of information currently available on direct effects of biological factors, such as competition, upon marsh plant growth. The model has been designed so that other factors that influence plant growth, such as soil nutrients, may be added as sufficient information becomes available. Interactions between factors, both positive and negative, may also be added when these are sufficiently understood.

Model Structure

119. Using these concepts, the model MARSH1 was formulated, and its general structure is shown in Figure 40. When a set of data is read into the program, it is immediately printed out with appropriate descriptions and formatting. The inputting data fully fall into three
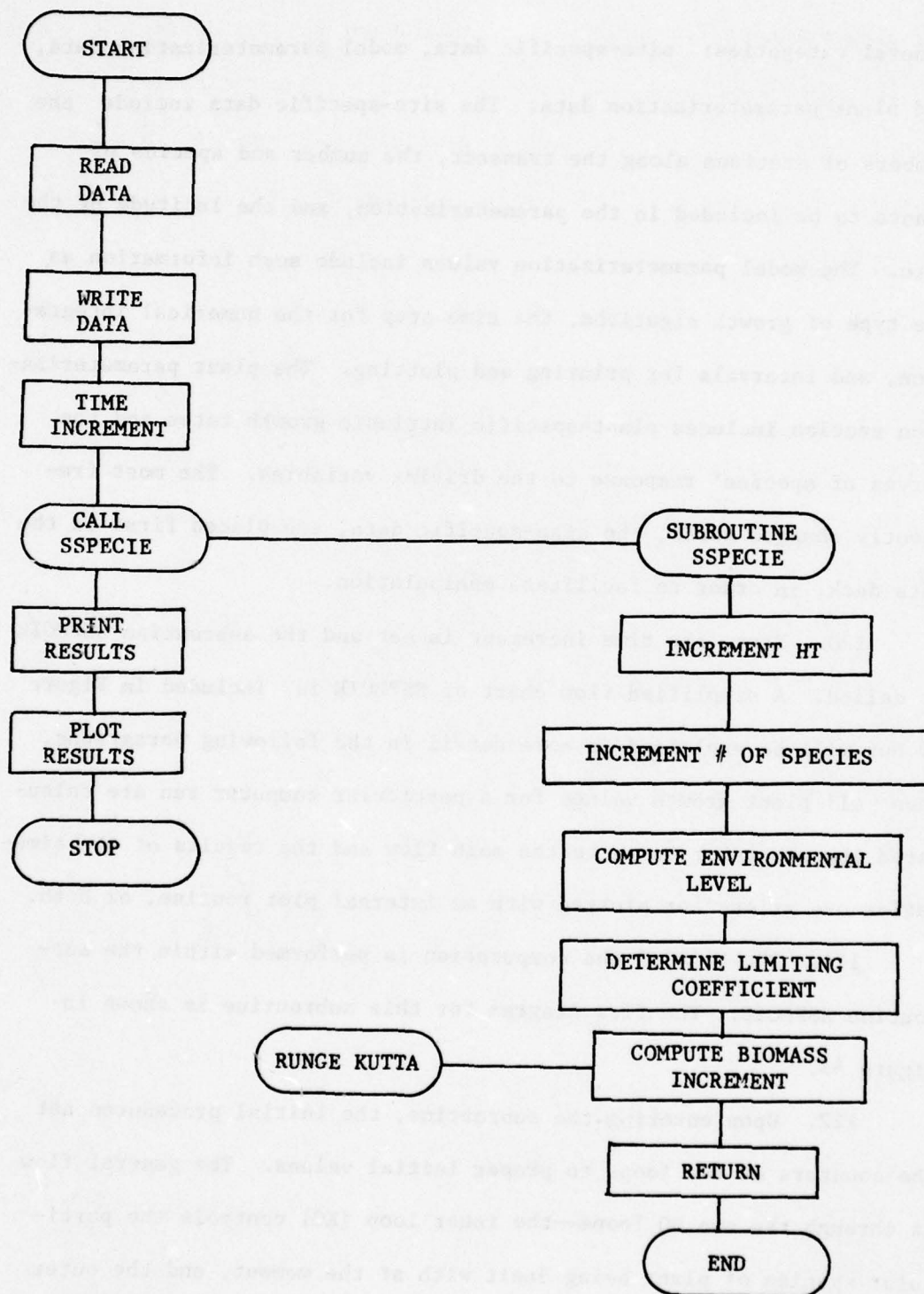
Figure 40. General flow diagram of the model, MARSH1.

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general categories: site-specific data, model parameterization data, and plant parameterization data. The site-specific data include the numbers of stations along the transect, the number and species of plants to be included in the parameterization, and the latitude of the site. The model parameterization values include such information as the type of growth algorithm, the time step for the numerical integration, and intervals for printing and plotting. The plant parameterization section includes plant-specific intrinsic growth rates and the curves of species' response to the driving variables. The most frequently changed cards, the site-specific data, are placed first in the data deck, in order to facilitate manipulation.

120. Next, the time increment is set and the subroutine SSPECIE is called. A simplified flow chart of SSPECIE is included in Figure 40 but will be explained in more detail in the following paragraphs. When all plant growth values for a particular computer run are calculated the program returns to the main flow and the results of the simulation are printed or plotted with an internal plot routine, or both.

121. The bulk of the computation is performed within the subroutine SSPECIE. The flow diagram for this subroutine is shown in Figure 41.

122. Upon entering the subroutine, the initial procedures set the counters of two loops to proper initial values. The general flow is through the two DO loops--the inner loop (KO) controls the particular species of plant being dealt with at the moment, and the outer loop (NN) determines the particular station on the marsh for which

```
        SUBROUTINE SSPECIE

        NN = NN + 1

        ZHT = HT(NN) + DEP(NN)

        KO = KO + 1

        FUNCTION LAT

        FUNCTION TEMP

        FUNCTION COHT

        FUNCTION COSHADE

        ZLIGHT = ZLIGHT * SHADE(KSPECIE)

        SUBROUTINE TIDE

        FUNCTION SAL

        DETERMINE LIMITING COEFF.
        FOR EACH PARAMETER

        DETERMINE MINIMUM
        LIMITING COEFFICIENT

        PMINB = PMIN*PEAKB(KSPECIE)

              PMINB < 0   ──YES──►  A = ((XXD(1)-)MINB/XXD(1))*.5
                  NO

        SUBROUTINE RUNGE
        YES
              KO < NUM
                  NO
        YES
              NN < NUMHT
                  NO
        RETURN
```
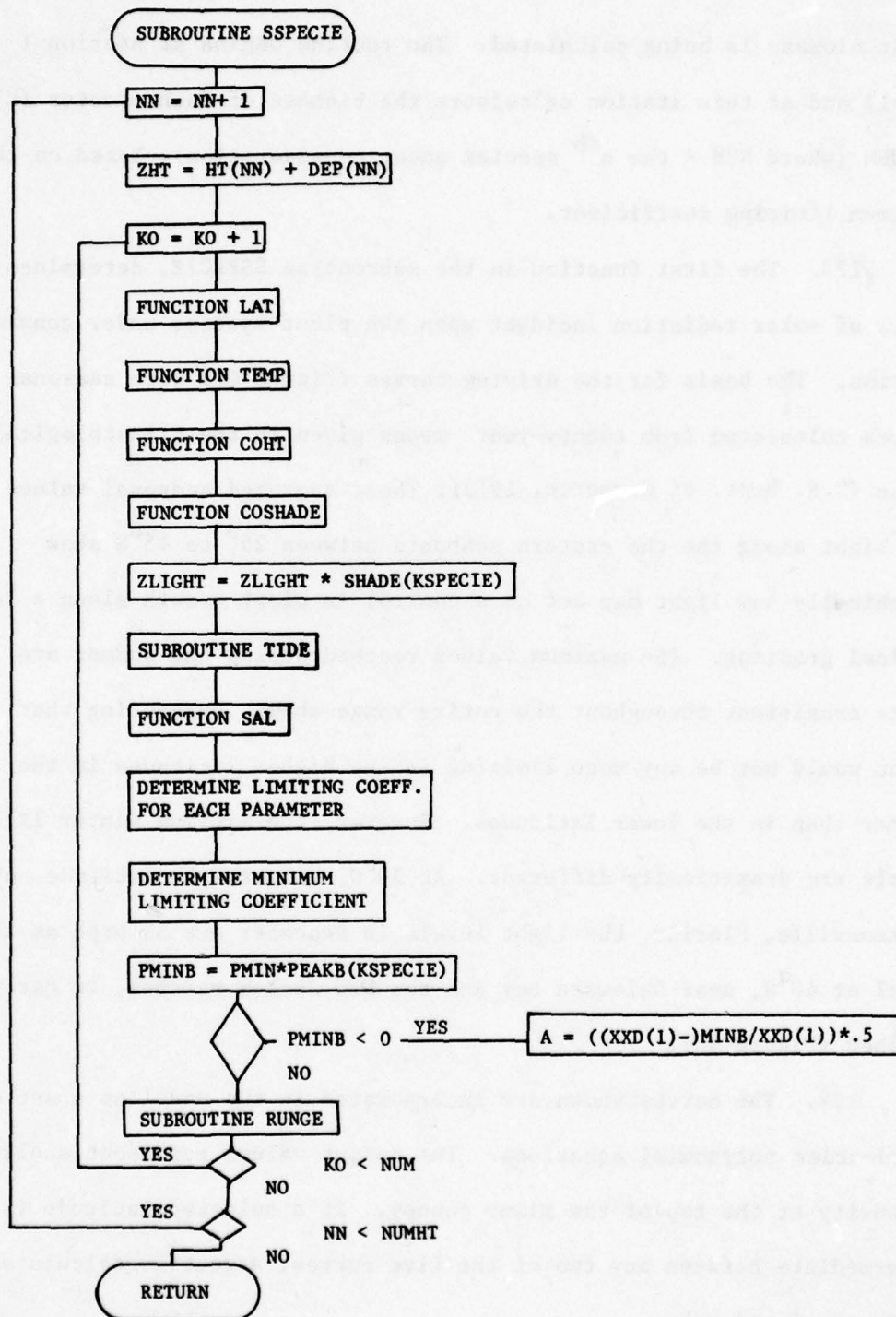
Figure 41. Flow diagram of the main subroutine, SSPECIE.

123

plant biomass is being calculated. The routine begins at station 1 (NN=1) and at this station calculates the biomass of each species (K)=L to NUM (where NUM = the nth species under consideration), based on the minimum limiting coefficient.

123. The first function in the subroutine SSPECIE, determines the level of solar radiation incident upon the plant species under consideration. The basis for the driving curves (Figure 42) were seasonal values calculated from twenty-year means given in the Climatological Atlas (U.S. Dept. of Commerce, 1973). These averaged seasonal values for light along the the eastern seaboard between 25° to 45°N show graphically how light may act as a control in plant growth along a latitudinal gradient. The maximum values reached during the summer are quite consistent throughout the entire range shown, suggesting that light would not be any more limiting in the higher latitudes in the summer than in the lower latitudes. However, the minimum winter light levels are dramatically different. At 30°N, roughly the latitude of Jacksonville, Florida, the light levels in December are as high as the level at 40°N, near Delaware Bay and the New Jersey marshes, in early October (Figure 42).

124. The curves shown are incorporated in the model as a set of third-order polynomial equations. The output values represent sunlight intensity at the top of the plant canopy. If a selected latitude is intermediate between any two of the five curves, a routine calculates an interpolated value.

125. Competition between plant species at a site is determined

124
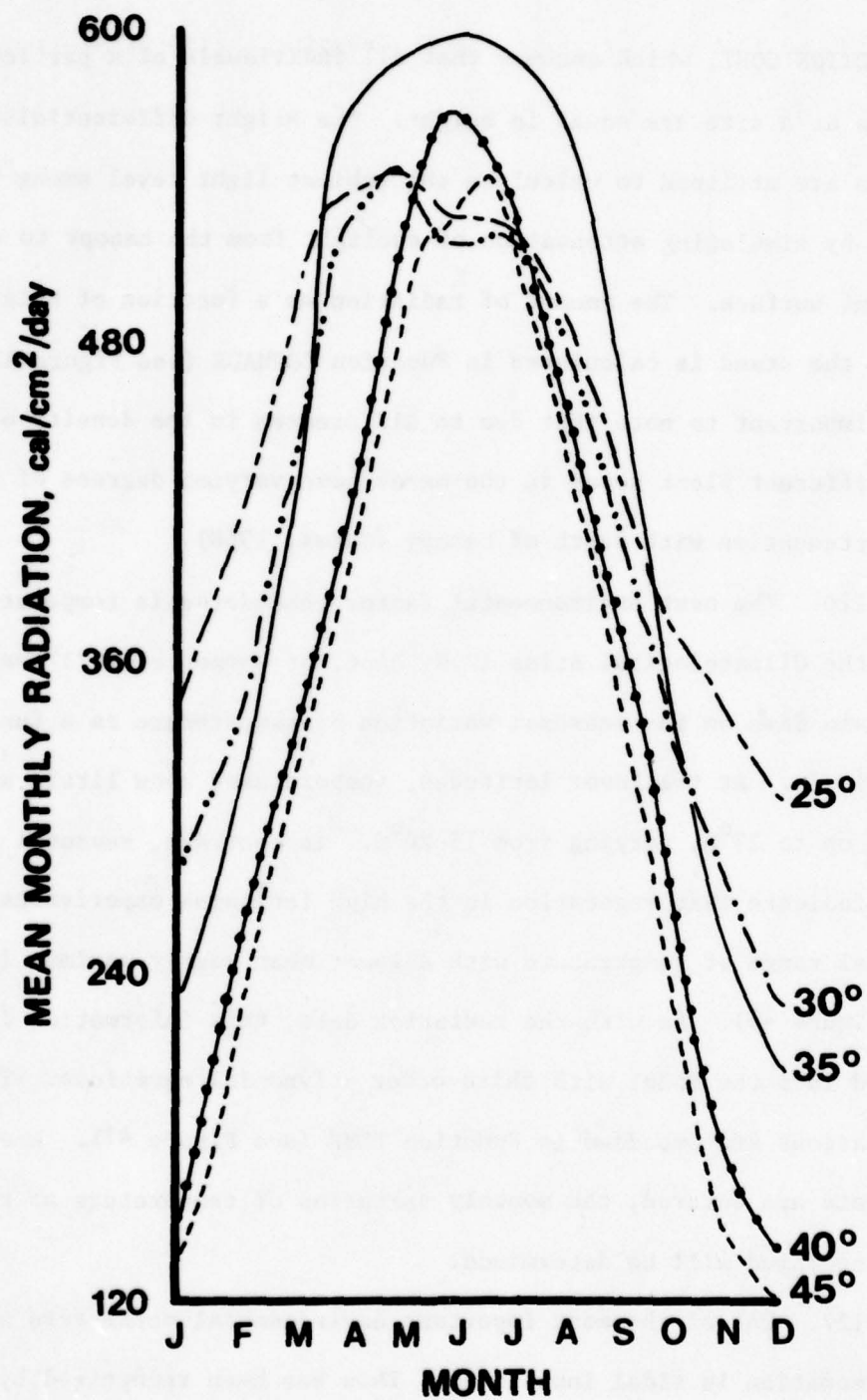
Figure 42. Seasonal solar radiation values for the eastern coast of the United States.

by FUNCTION COHT, which assumes that all individuals of a particular species at a site are equal in height. The height differentials among species are utilized to calculate the ambient light level among the plants by simulating attenuation of sunlight from the canopy to the sediment surface. The amount of radiation as a function of height within the stand is calculated in Function COSHADE (see Figure 41). It is important to note that due to differences in the density of foliage, different plant zones in the marsh have varying degrees of radiation attenuation with depth of canopy (Gates, 1968).

126. The next environmental factor considered is temperature. Again the Climatological Atlas (U.S. Dept. of Commerce, 1973) was used to obtain data on the seasonal variation of temperature as a function of latitude. At the lower latitudes, temperatures show little seasonal change up to 27°N, varying from $15-20^{o}$C. In contrast, seasonal temperatures indicate that vegetation in the high latitudes experiences a wide seasonal range of temperature with a lower mean yearly maximum ($16-22^{o}$C) (see Figure 43). As with the radiation data, this information is incorporated into the model with third-order polynomial equations. These formulations are embedded in Function TEMP (see Figure 41). When latitude data are entered, the monthly variation of temperature at the location specified will be determined.

127. One of the most important environmental parameters affecting plant zonation is tidal inundation. This has been recognized by numerous investigators and was further substantiated in other sections of this report. It was shown herein that tidal inundation is the most

126
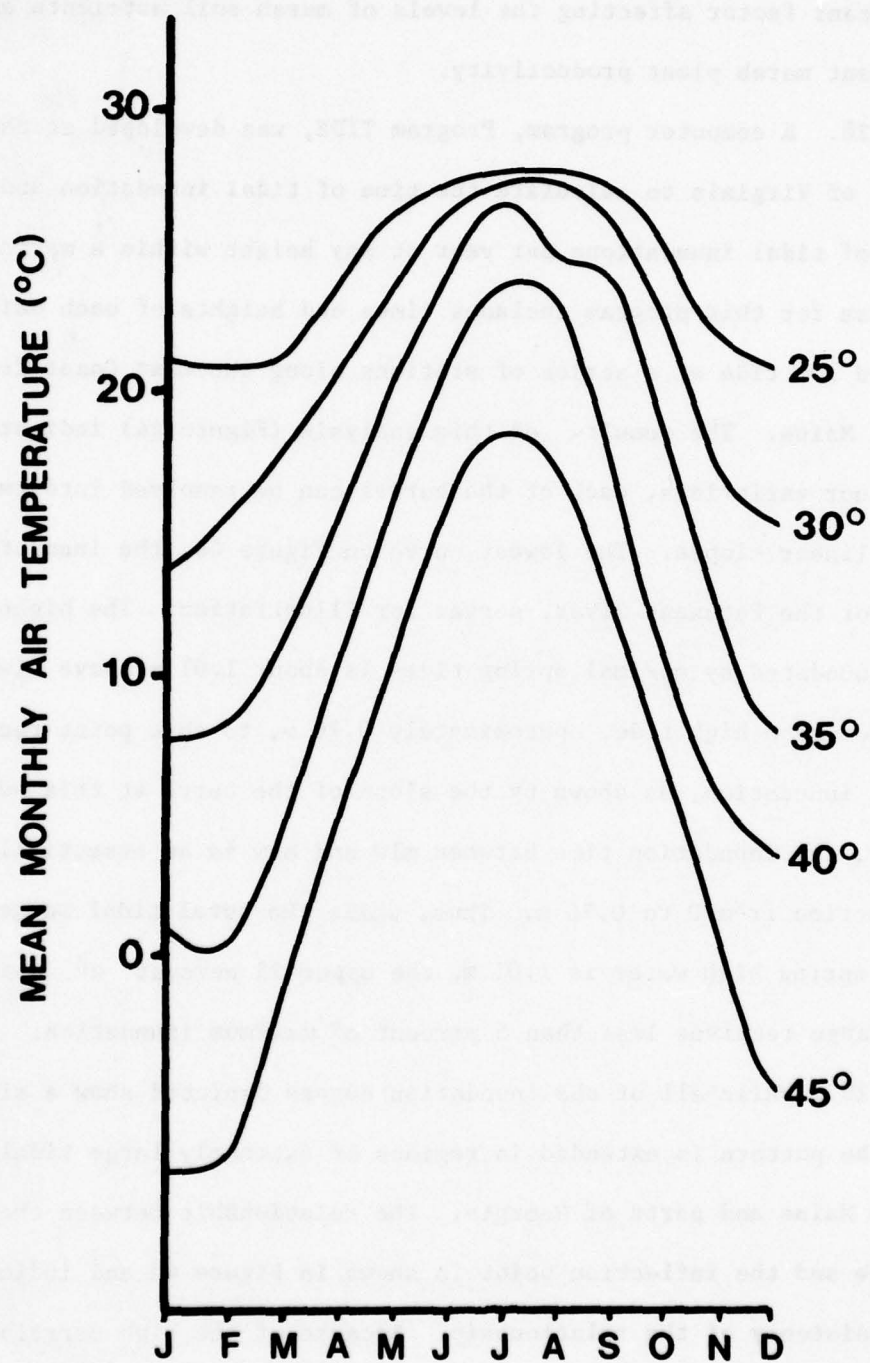
Figure 43.   Seasonal temperature values for the
eastern coast of the United States.

significant factor affecting the levels of marsh soil nutrients and the resultant marsh plant productivity.

128. A computer program, Program TIDE, was developed at the University of Virginia to calculate the time of tidal inundation and the number of tidal inundations per year at any height within a marsh. The data base for this program includes times and heights of each daily high and low tide at a series of stations along the East Coast from Key West to Maine. The results of this analysis (Figure 44) indicate that, with minor variations, each of the curves can be resolved into two nearly linear slopes. The lowest curve on Figure 44, the inundation curve for the Patuxent River, serves for illustration. The highest point inundated by maximal spring tides is about 1.01 m above mlw. The area from mean high tide, approximately 0.76 m, to this point receives minimal inundation, as shown by the slope of the curve at this point. However, the inundation time between mlw and mhw is an essentially linear function from 0 to 0.76 m. Thus, while the total tidal range from mlw to spring high water is 1.01 m, the upper 25 percent of the tidal range receives less than 5 percent of maximum inundation.

129. While all of the inundation curves depicted show a similar form, the pattern is extended in regions of extremely large tidal ranges, such as Maine and parts of Georgia. The relationship between the maximum tide and the inflection point is shown in Figure 45 and indicates the consistency of the relationship. Because of the high correlation between the inflection point and the maximum tidal height, the series of curves for tidal inundation can be condensed into a normalized

128
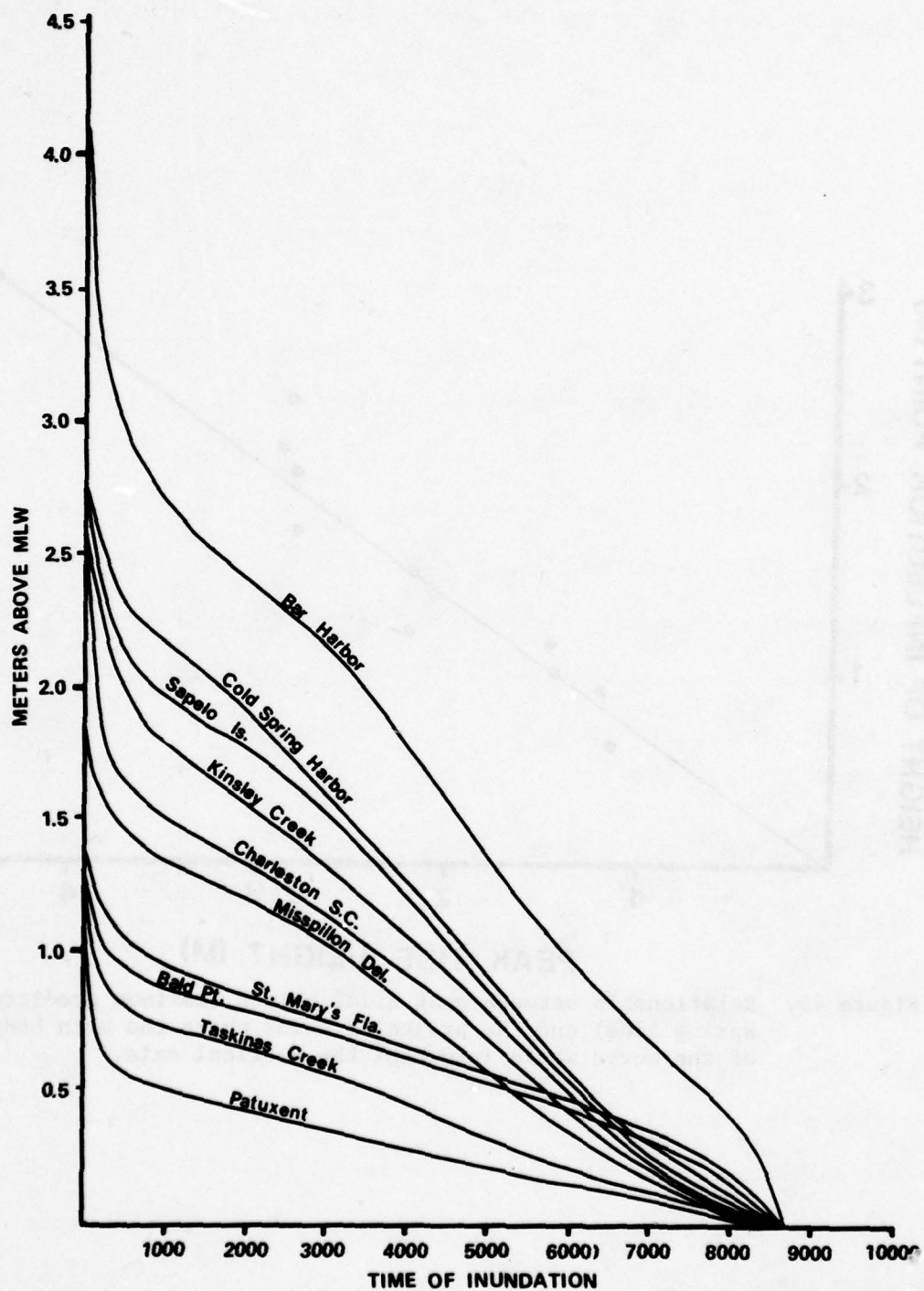
Figure 44. Inundation curves at various stations on the Atlantic and Gulf coasts.
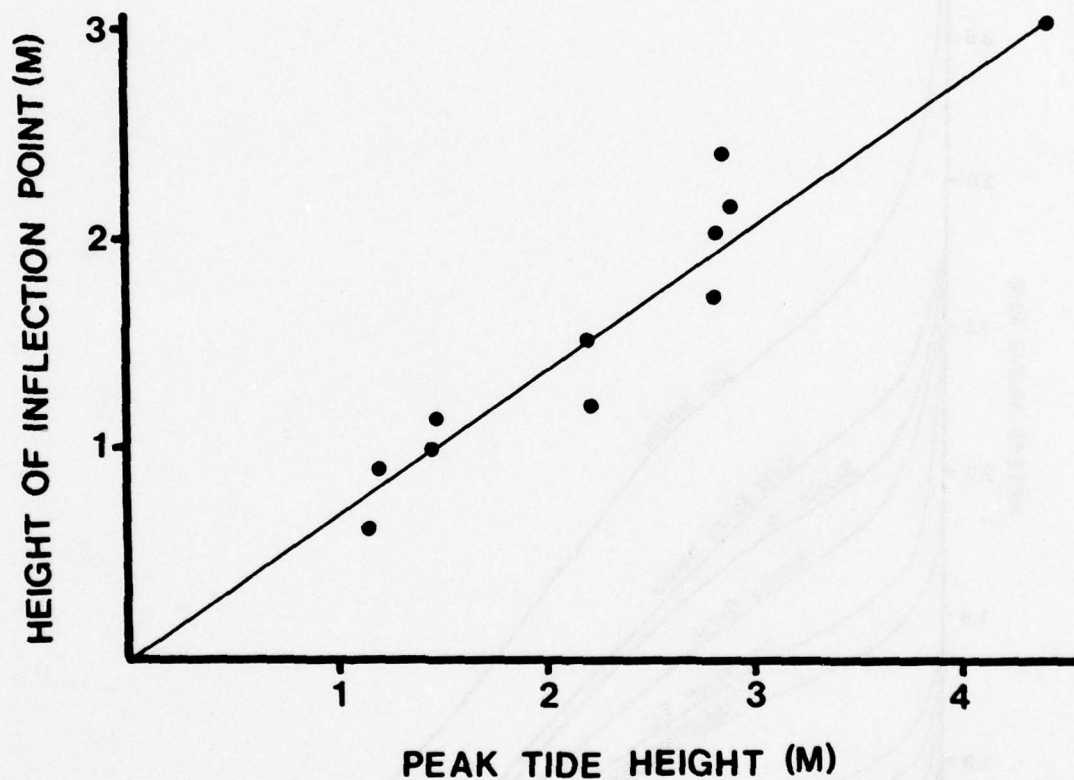
Figure 45. Relationship between peak tidal height (maximum predicted spring tide) and the projected point where the main body of the curve would intercept the vertical axis.

relationship (Figure 46) by taking each curve from Figure 44 separately and dividing the value on each axis by the maximum value for that site relating both the height and inundation values of percent of minimum. The normalized curve (Figure 46) permits calculation of the time of inundation given the height of the station of interest and height of the spring tides above mlw. The inflection point in the normalized curve occurs at 75 percent of the maximum tidal height and corresponds to mhw. This is also the level on a marsh where the interface between the S. alterniflora zone and S. patens – D. spicata zone usually occurs. The region above mhw is inundated less than 4 percent of the year.

130. Within the succession model, the relationship between relative height and percent inundation is represented by a piecewise linear formulation embedded in subroutine TIDE.

131. The final environmental parameter considered is soil salinity. Figure 12 shows changes in soil salinity along a series of transects in Bennett's and Taskinas marshes. Salinity in the hydrologically active low marsh is comparable to that found in the contiguous marsh creek. Higher salinity is found at higher elevations above mlw. This trend is simulated in the model by a piecewise linear formulation (Figure 47), which is represented by graphing relative height in a marsh (station height/mean tidal range) versus salinity. This graph shows that an increase in elevations on the marsh surface results in a soil salinity nearly double that found in the nearby marsh creek; the difference may be caused by evaporation and possibly by water loss due to transpiration. Where the marsh borders the upland, freshwater runoff dilutes soil salinity to almost 0 ppt.

131
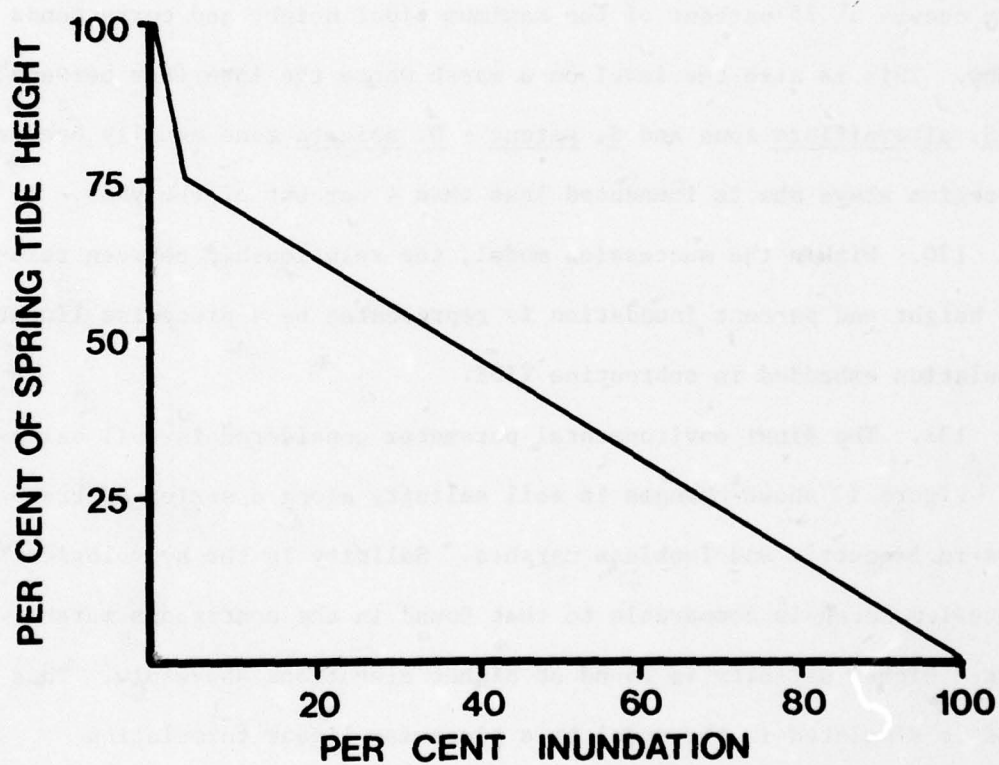
Figure 46. Normalized curve for tidal inundation as a function of height of maximum spring tide.
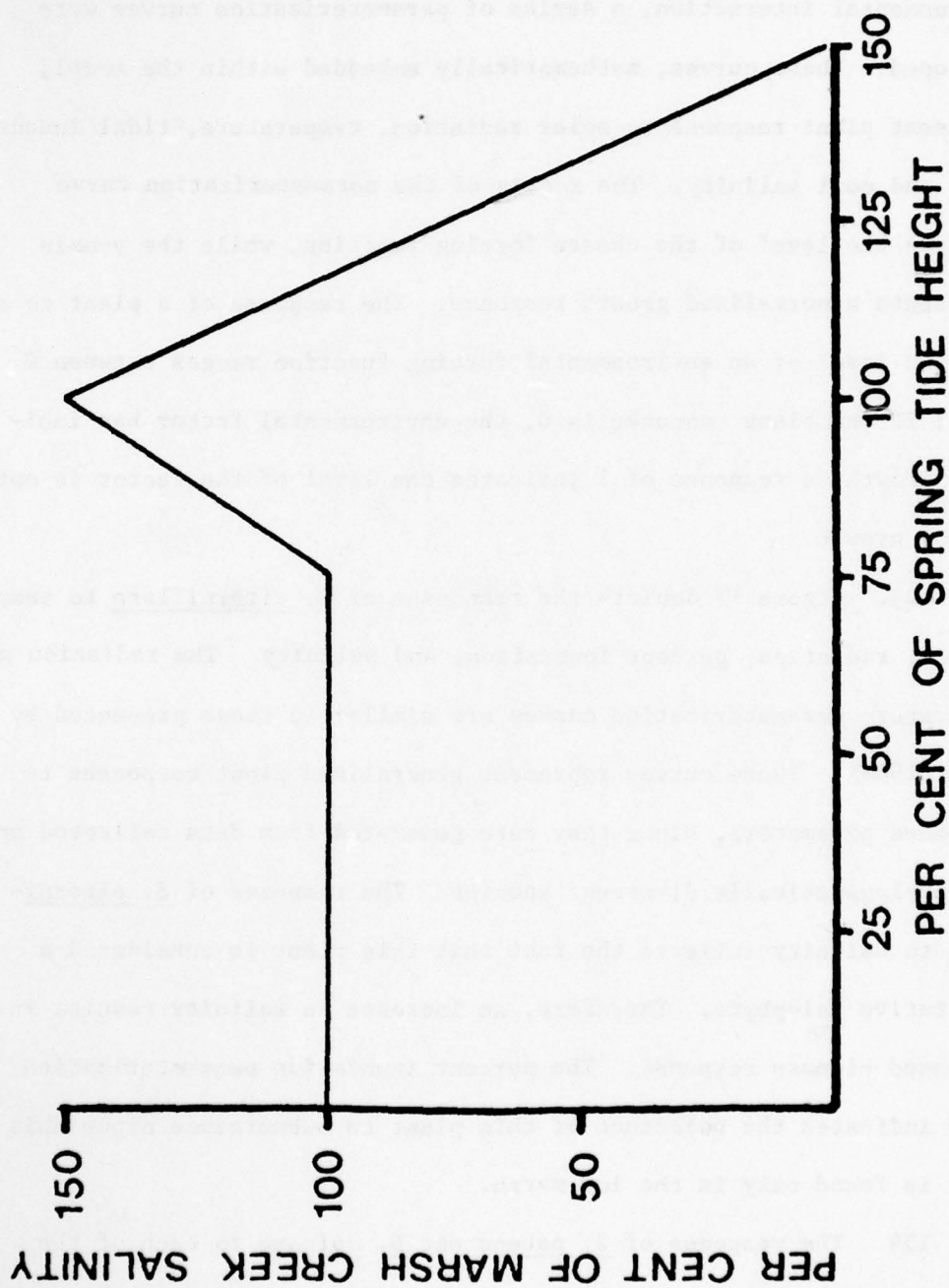
Figure 47. Marsh salinity as a function of tidal height.

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132. In order to determine how much each species is curtailed by environmental interaction, a series of parameterization curves were developed. These curves, mathematically embedded within the model, represent plant response to solar radiation, temperature, tidal inundation, and soil salinity. The x-axis of the parameterization curve reflects the level of the chosen forcing function, while the y-axis represents a normalized growth response. The response of a plant to a specific level of an environmental forcing function ranges between 0 and 1; if the plant response is 0, the environmental factor has inhibited growth; a response of 1 indicates the level of the factor is optimum for growth.

133. Figure 48 depicts the responses of S. alterniflora to temperature, radiation, percent inundation, and salinity. The radiation and temperature parameterization curves are similar to those presented by Gates (1968). These curves represent generalized plant responses to the above parameters, since they were generated from data collected on many phylogenetically divergent species. The response of S. alterniflora to salinity reflects the fact that this plant is considered a facultative halophyte. Therefore, an increase in salinity results in a decreased biomass response. The percent inundation parameterization curve indicates the tolerance of this plant to submergence since this plant is found only in the low marsh.

134. The response of S. patens and D. spicata to each of the environmental parameters is depicted in Figure 49. Competition between the species is not modeled explicitly; however, the data do reflect natural situations. Lacking data to the contrary, the parameterization

134
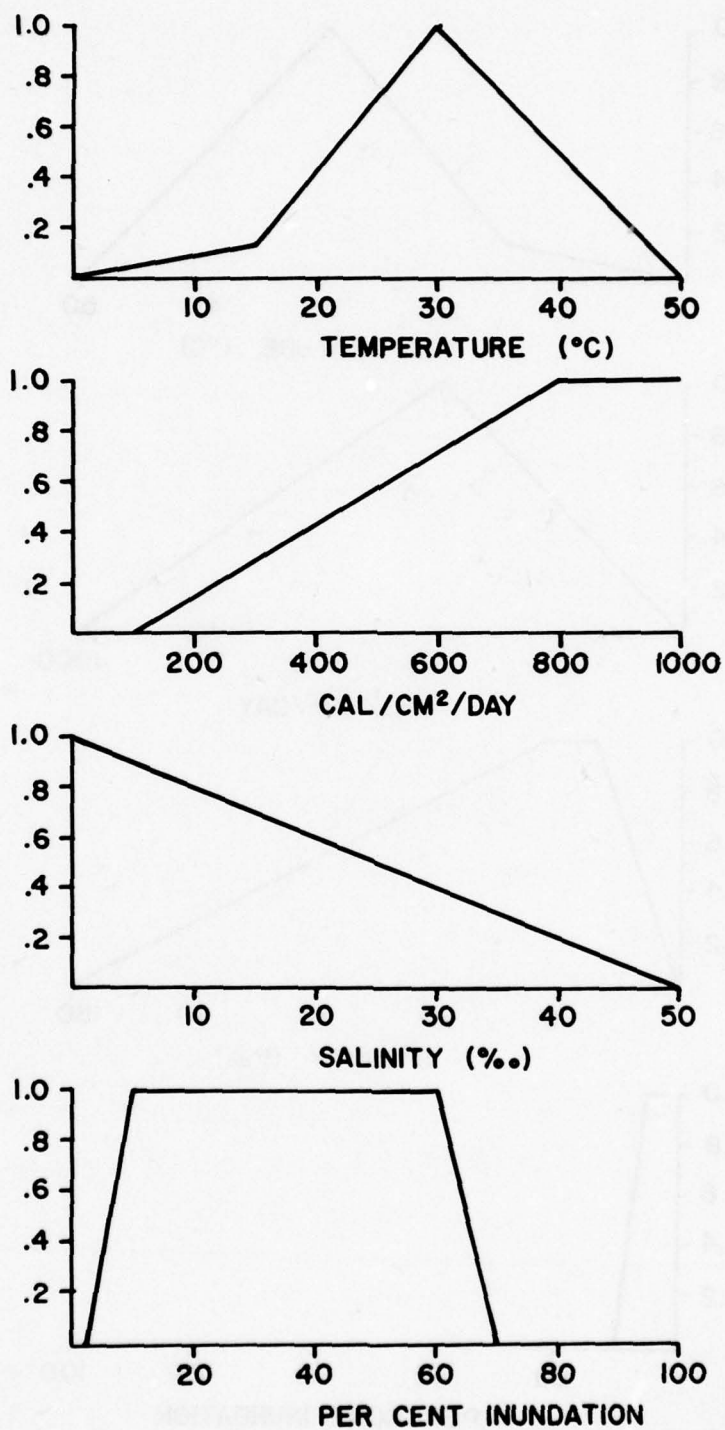
Figure 48. Normalized growth response of _Spartina alterniflora_ to environmental driving parameters.
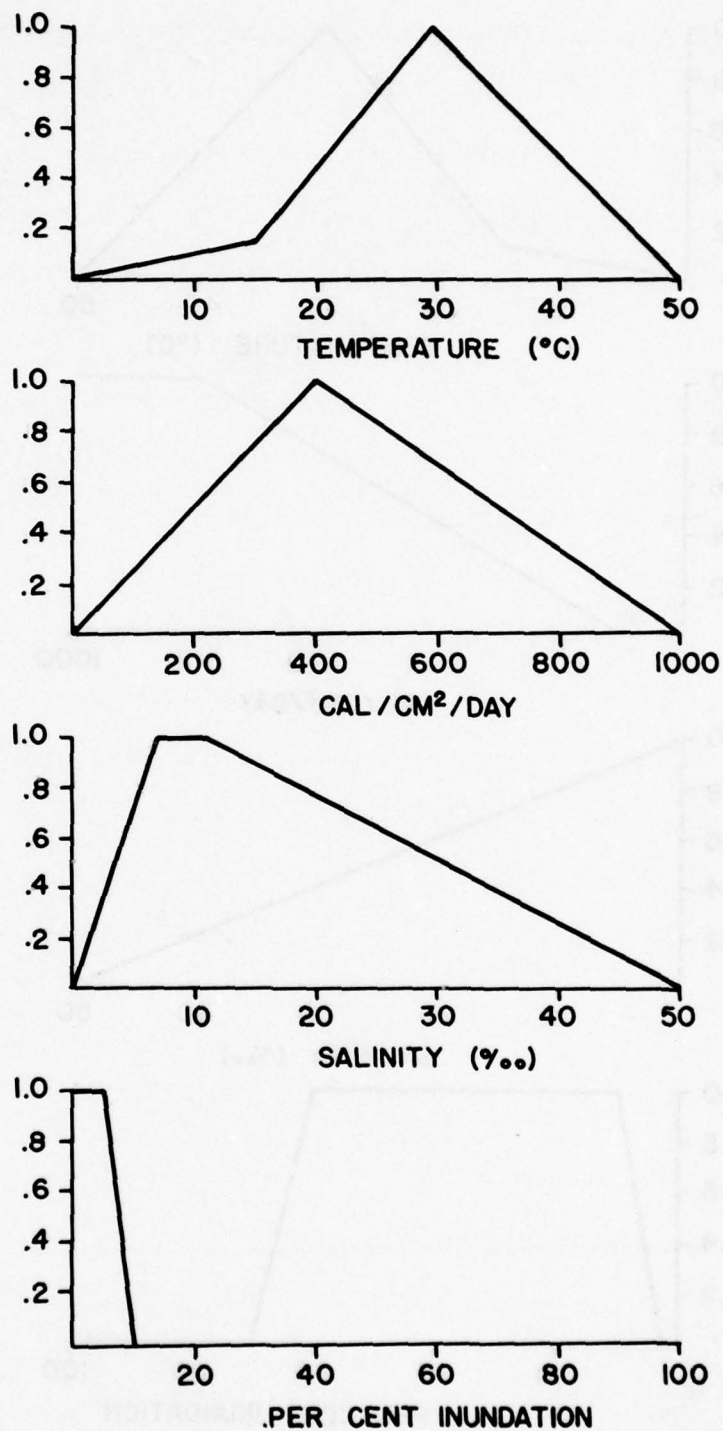
Figure 49. Normalized growth response of _Spartina patens_ and _Distichlis spicata_ to environmental driving parameters.

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curves for radiation and temperature are assumed to be identical to those of S. alterniflora. However, the actual responses of S. alterniflora and S. patens are not identical, since their heights and the resultant shading effects are usually quite different. It was assumed that S. patens is better adapted to higher salinities since it is found in the high marsh. This is reflected in the salinity parameterization curve. Similarly, as a result of its position in the marsh, maximum growth response of S. patens to percent inundation was found at a lower value than that of S. alterniflora.

135. D. spicata and S. patens have similar responses to the four environmental parameters (Figure 49). The difference lies in the fact that the tolerance to salinity and percent inundation of D. spicata is greater than that of S. patens. Parameterization curves for S. alterniflora, S. patens, and D. spicata have been discussed because these three plants dominate the marsh vegetation in many localities, but curves for any other species can be formulated if the necessary field data are available.

136. At this point in the program a plant response value or limiting coefficient is determined for each species and each environmental factor. The assumption that certain environmental parameters are largely responsible for restricting growth (law of the minimum) simplifies the task of determining the relative effect of the limiting factors. At each calculation the limiting factor is stored, so that the operator may recall at any time the parameter that is limiting a particular species. With this information, a Runge-Kutta numerical

integrating subroutine is accessed to calculate plant productivity. Within this subroutine two options for calculating productivity are available: a logistic method and a maximum productivity method. Several assumptions are inherent in using these methods. In the logistic formulations productivity is determined as a function of the intrinsic growth rate, the limiting coefficient, and the contemporaneous biomass. Also included is a negative feedback term associated with environmental inhibition. The maximum productivity algorithm is the product of the limiting coefficient multiplied by maximum productivity per unit time. Within this model alterations are made for relative elevation and all species of interest. The output yields plotted and printed biomass estimates for each species as a function of time and space.

137. As described above, the marsh model is composed of a series of point models that are linked spatially (Figure 40). The real world basis of this linkage is the lateral transport of water-borne sediments. Within the model, relative elevation in the marsh controls, to a great extent, the interaction between plant and environment. At each location in the marsh, allowance is made for a temporal increment of sediment, and the resulting changes in elevation control the spatial distribution of plant species.

138. The above discussion serves to illustrate the logic and assumptions inherent in the succession model. A complete listing of the model, with detailed instructions on assembly of the data cards and use, is contained in Appendix B. Using only the parameterization curves given for the three species utilized, a vast number of simulations are possible. The following discussion will illustrate the

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results of one set of simulations.

139. For these experimental simulations, latitude and tidal range were varied to study the effect of elevation on plant growth and species location on the marsh surface. The first simulation (Figures 50-55), the growth of plants on salt marsh at latitude 30°N, with a tidal creek salinity of 20 o/oo, a spring tidal range of 1.83 m, and a mean tidal range of 1.3 m was depicted at stations varying from 0.31 to 1.33 m above mlw. The three letters at the right-hand side of the figure illustrate which of the four environmental variables was limiting for each species (T = temperature, H = tidal height, S = salinity, and L = light). The first letter refers to the environmental variable limiting the first species listed, the second letter refers to the second species, and the third letter refers to the third species.

140. S. alterniflora was found growing in the low marsh as expected with growth beginning at 0.62 m above mlw or near the mean tidal height. With an increase in elevation, the pure stand of S. alterniflora graded into a mixed association including S. patens and D. spicata near the mean high tide mark. On Figures 50-55, the graphs indicate species 1 (S. alterniflora) and 3 (D. spicata) only. S. patens (#2) was present but had the same value as D. spicata. When this occurs, the plotting routine prints the single highest species number encountered. In the high marsh above mlw only S. patens and D. spicata were found. In this simulation, S. patens and D. spicata were excluded from the low marsh due to excessive inundation, while growth on the high marsh for these plants was most limited due to light and temperature.

141. In the second simulation shown here (Figures 56-60), the

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PLANT BIOMASS
200.0   400.0   600.0   800.0   1000.0   PHINCO

LATITUDE = 30.   CREEK SAL = 20.

MEAN TIDE = 4.   SPRING TIDE = 6.   MARSH HEIGHT = 1.
PLANT1 = S ALT   R = 4.   PEAK STANDING CROP = 1200.
PLANT2 = D SPICATA   R = 5.   PEAK STANDING CROP = 600.
PLANT3 = S PATENS   R = 5.   PEAK STANDING CROP = 600.

Figure 50. Results of a simulation at latitude 30°N, with a creek salinity of 20 o/oo, a mean tide range of 6 ft (1.83 m), a maximum range of 4 ft (1.22 m), and a time period of 48 months. This first figure depicts the simulation at the 1-ft (0.31-m) elevation above mlw on the marsh.

PLANT BIOMASS

| | 200.0 | 400.0 | 600.0 | 800.0 | 1000.0 | PRIMCB |

LATITUDE = 30.   CREEK SAL = 20.

MEAN TIDE = 4.   SPRING TIDE = 4.   MARSH HEIGHT = 2.

PLANT1 = S ALT   R = 4.   PEAK STANDING CROP = 1200.
PLANT2 = D SPICATA   R = 5.   PEAK STANDING CROP = 600.
PLANT3 = S PATENS   R = 5.   PEAK STANDING CROP = 600.

Figure 51. Depicts the simulation at the 2-ft (0.61-m) elevation above mlw on the marsh.

PLANT BIOMASS

200.0   400.0   600.0   800.0   1000.0   PRINCO

1. RON   TTT
2. RON   1   THH
3. RON   1   THH
4. RON   1   THH
5. RON   1   SHH
6. RON   1   SHH
7. RON   1   SHH
8. RON   1   LHH
9. RON   1   LHH
10. RON   1   THH
11. RON   1   THH

LATITUDE = 30. CREEK SAL = 20.

12. RON   1   TTT
13. RON   1   TTT

MEAN TIDE = 4. SPRING TIDE = 6. MARSH HEIGHT = 3.

PLANT1 = S ALT   R = 4. PEAK STANDING CROP = 1200.
PLANT2 = D SPICATA   R = 5. PEAK STANDING CROP = 600.
PLANT3 = S PATENS   R = 5. PEAK STANDING CROP = 600.

14. RON   1   THH
15. RON   1   THH
16. RON   1   THH
17. RON   1   SHH
18. RON   1   SHH
19. RON   1   SHH
20. RON   1   LHH
21. RON   1   LHH
22. RON   1   THH
23. RON   1   THH
24. RON   1   TTT
25. RON   1   TTT
26. RON   1   THH
27. RON   1   THH
28. RON   1   THH
29. RON   1   SHH
30. RON   1   SHH
31. RON   1   SHH
32. RON   1   LHH
33. RON   1   LHH
34. RON   1   THH
35. RON   1   THH
36. RON   1   TTT
37. RON   1   TTT
38. RON   1   THH
39. RON   1   THH
40. RON   1   THH
41. RON   1   SHH
42. RON   1   SHH
43. RON   1   SHH
44. RON   1   LHH
45. RON   1   LHH
46. RON   1   THH
47. RON   1   THH
48. RON   1   TTT

Figure 52. Depicts the simulation at the 3-ft (0.91-m) elevation above mlw on the marsh.

PLANT BIOMASS
```
            200.0        400.0        600.0        800.0       1000.0   PRINCO

 1. MON •···················································•···········   TTT
 2. MON     1 3                                                          TTT
 3. MON         3              1          LATITUDE = 30.   CREEK SAL = 20.   MTT
 4. MON •          3       1              MEAN TIDE = 4.   SPRING TIDE = 6.   MARSH HEIGHT = 4.   LTT
 5. MON •       1       3                 PLANT1 = S ALT      R = 4.   PEAK STANDING CROP = 1200.   LTT
                                          PLANT2 = D SPICATA  R = 5.   PEAK STANDING CROP = 600.
 6. MON •   1              3              PLANT3 = S PATENS   R = 5.   PEAK STANDING CROP = 600.   LTT
 7. MON •  1                 3                                           LTT
 8. MON •  1                3                                            LTT
 9. MON •  1             3                                               LTT
10. MON •  1       3                                                     LTT
11. MON •     1 3                                                        LTT
12. MON • 31                                                             TTT
13. MON • 31                                                             TTT
14. MON •      3   1                                                     TTT
15. MON •      3        1                                                MTT
16. MON •         3      1                                               LTT
17. MON •       1      3                                                 LTT
18. MON •   1              3                                             LTT
19. MON •   2               3                                            LTT
20. MON •  1               3                                             LTT
21. MON •  1             3                                               LTT
22. MON •  1        3                                                    LTT
23. MON •     1 3                                                        LTT
24. MON • 31                                                             TTT
25. MON • 31                                                             TTT
26. MON •      3   1                                                     TTT
27. MON •       3          1                                             MTT
28. MON •          3      1                                              LTT
29. MON •        3      3                                                LTT
30. MON •   1               3                                            LTT
31. MON •  1                3                                            LTT
32. MON •  1               3                                            LTT
33. MON •  1              3                                              LTT
34. MON •   1       3                                                    LTT
35. MON •     1 3                                                        LTT
36. MON • 31                                                             TTT
37. MON • 31                                                             TTT
38. MON •      3   1                                                     TTT
39. MON •        3        1                                              MTT
40. MON •           3      1                                             LTT
41. MON •        1      3                                                LTT
42. MON •   1                3                                           LTT
43. MON •  1                 3                                           LTT
44. MON •  1                3                                            LTT
45. MON •  2              3                                              LTT
46. MON •   1      3                                                     LTT
47. MON •     1 3                                                        LTT
48. MON • 31                                                             TTT
```

Figure 53. Depicts the simulation at the 4-ft (1.22-m) elevation above mlw on the marsh.

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PLANT BIOMASS

| | 200.0 | 400.0 | 600.0 | 800.0 | 1000.0 | PRIMCO |

1. MON •···•·········•········•······• TTT

LATITUDE = 30.   CREEK SAL = 20.

2. MON • 3   MTT

3. MON •   3   MEAN TIDE = 4.   SPRING TIDE = 6.   MARSH HEIGHT = 9.   MTT

PLANT1 = S ALT   R = 4.   PEAK STANDING CROP = 1200.
PLANT2 = D SPICATA R = 5.   PEAK STANDING CROP = 600.
PLANT3 = S PATENS R = 5.   PEAK STANDING CROP = 600.

4. MON •   3   MTT
5. MON •   3   MTT
6. MON •   3   MTT
7. MON •   3   MTT
8. MON •   3   MTT
9. MON •   3   MTT
10. MON •   3   MTT
11. MON •   3   MTT
12. MON • 3   TTT
13. MON • 3   TTT
14. MON •   3   MTT
15. MON •   3   MTT
16. MON •   3   MTT
17. MON •   3   MTT
18. MON •   3   MTT
19. MON •   3   MTT
20. MON •   3   MTT
21. MON •   3   MTT
22. MON •   3   MTT
23. MON •   3   MTT
24. MON • 3   TTT
25. MON • 3   TTT
26. MON •   3   MTT
27. MON •   3   MTT
28. MON •   3   MTT
29. MON •   3   MTT
30. MON •   3   MTT
31. MON •   3   MTT
32. MON •   3   MTT
33. MON •   3   MTT
34. MON •   3   MTT
35. MON •   3   MTT
36. MON • 3   TTT
37. MON • 3   TTT
38. MON •   3   MTT
39. MON •   3   MTT
40. MON •   3   MTT
41. MON •   3   MTT
42. MON •   3   MTT
43. MON •   3   MTT
44. MON •   3   MTT
45. MON •   3   MTT
46. MON •   3   MTT
47. MON •   3   MTT
48. MON • 3   TTT

Figure 54. Depicts the simulation at the 5-ft (1.52-m) elevation above mlw on the marsh.

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PLANT BIOMASS

| | 200.0 | 400.0 | 600.0 | 800.0 | 1000.0 | PRINCO |

LATITUDE = 30. CREEK SAL = 20.

MEAN TIDE = 4. SPRING TIDE = 6. MARSH HEIGHT = 6.

PLANT1 = S ALT   B = 4. PEAK STANDING CROP = 1200.
PLANT2 = D SPICATA B = 5. PEAK STANDING CROP = 600.
PLANT3 = S PATENS   B = 9. PEAK STANDING CROP = 600.

Figure 55. Depicts the simulation at the 6-ft (1.83-m) elevation above mlw on the marsh.

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PLANT BIOMASS

| | 200.0 | 400.0 | 600.0 | 800.0 | 1000.0 | PHIRCO |

LATITUDE = 35. CREEK SAL = 20.

MEAN TIDE = 4. SPRING TIDE = 6. MARSH HEIGHT = 2.

PLANT1 = S ALT   R = 4. PEAK STANDING CROP = 1200.
PLANT2 = D SPICATA R = 5. PEAK STANDING CROP = 600.
PLANT3 = S PATENS   R = 5. PEAK STANDING CROP = 600.

Figure 56. Results of a simulation at latitude 35°N, with a creek salinity of 20 o/oo, a mean tide range of 4 ft (1.22 m), and a maximum range of 6 ft (1.83 m), for 48 months. This figure depicts the simulation at the 2-ft (0.61-m) elevation above mlw on the marsh.

PLANT BIOMASS

| | 200.0 | 400.0 | 600.0 | 800.0 | 1000.0 | PRIMCO |

```
 1. RON ●..................................................................●  TTT
 2. RON ●:                                                                   TTT
                    LATITUDE = 35.  CREEK SAL = 20.
 3. RON ●:                                                                   TTT
                    MEAN TIDE = 4.  SPRING TIDE = 6.  MARSH HEIGHT = 3.
                    PLANT1 = S ALT      R = 4.  PEAK STANDING CROP = 1200.
 4. RON ● 1         PLANT2 = D SPICATA  R = 5.  PEAK STANDING CROP = 600.    TNH
                    PLANT3 = S PATENS   R = 5.  PEAK STANDING CROP = 600.
 5. RON ●:                      1                                            TNH
 6. RON ●:                              1                                    SNH
 7. RON ●:                              1                                    SNH
 8. RON ●:                              1                                    SNH
 9. RON ●:                          1                                        TNH
10. RON ●:           1                                                       TNH
11. RON ●: 1                                                                 TTT
12. RON ●:                                                                   TTT
13. RON ●:                                                                   TTT
14. RON ●:                                                                   TTT
15. RON ●:                                                                   TTT
16. RON ● 1                                                                  TNH
17. RON ●:                      1                                            TNH
18. RON ●:                              1                                    SNH
19. RON ●:                              1                                    SNH
20. RON ●:                              1                                    SNH
21. RGN ●:                          1                                        TNH
22. RON ●:           1                                                       TNH
23. RON ● 1                                                                  TTT
24. RGN ●:                                                                   TTT
25. RON ●:                                                                   TTT
26. RON ●:                                                                   TTT
27. RON ●:                                                                   TTT
28. RON ●: 1                                                                 TNH
29. RON ●:                      1                                            TNH
30. RON ●:                              1                                    SNH
31. RON ●:                              1                                    SNH
32. RON ●:                              1                                    SNH
33. RON ●:                          1                                        TNH
34. RON ●:           1                                                       TNH
35. RON ● 1                                                                  TTT
36. RON ●:                                                                   TTT
37. RON ●:                                                                   TTT
38. RON ●:                                                                   TTT
39. RON ●:                                                                   TTT
40. RON ● 1                                                                  TNH
41. RGN ●:                      1                                            TNH
42. RGN ●:                              1                                    SNH
43. RON ●:                              1                                    SNH
44. RON ●:                              1                                    SNH
45. RON ●:                          1                                        TNH
46. RGN ●:           1                                                       TNH
47. RON ● 1                                                                  TTT
48. RON ●:                                                                   TTT
```
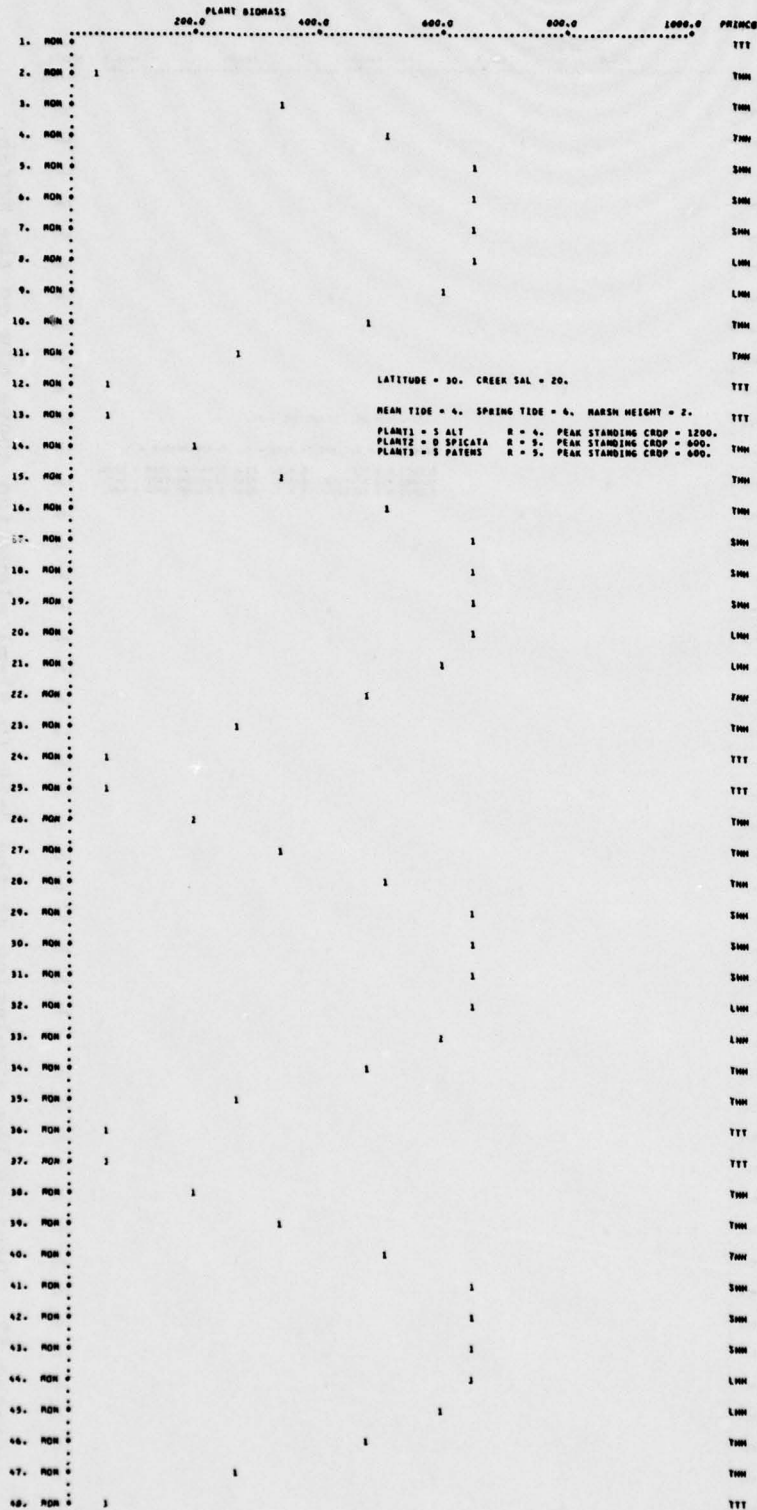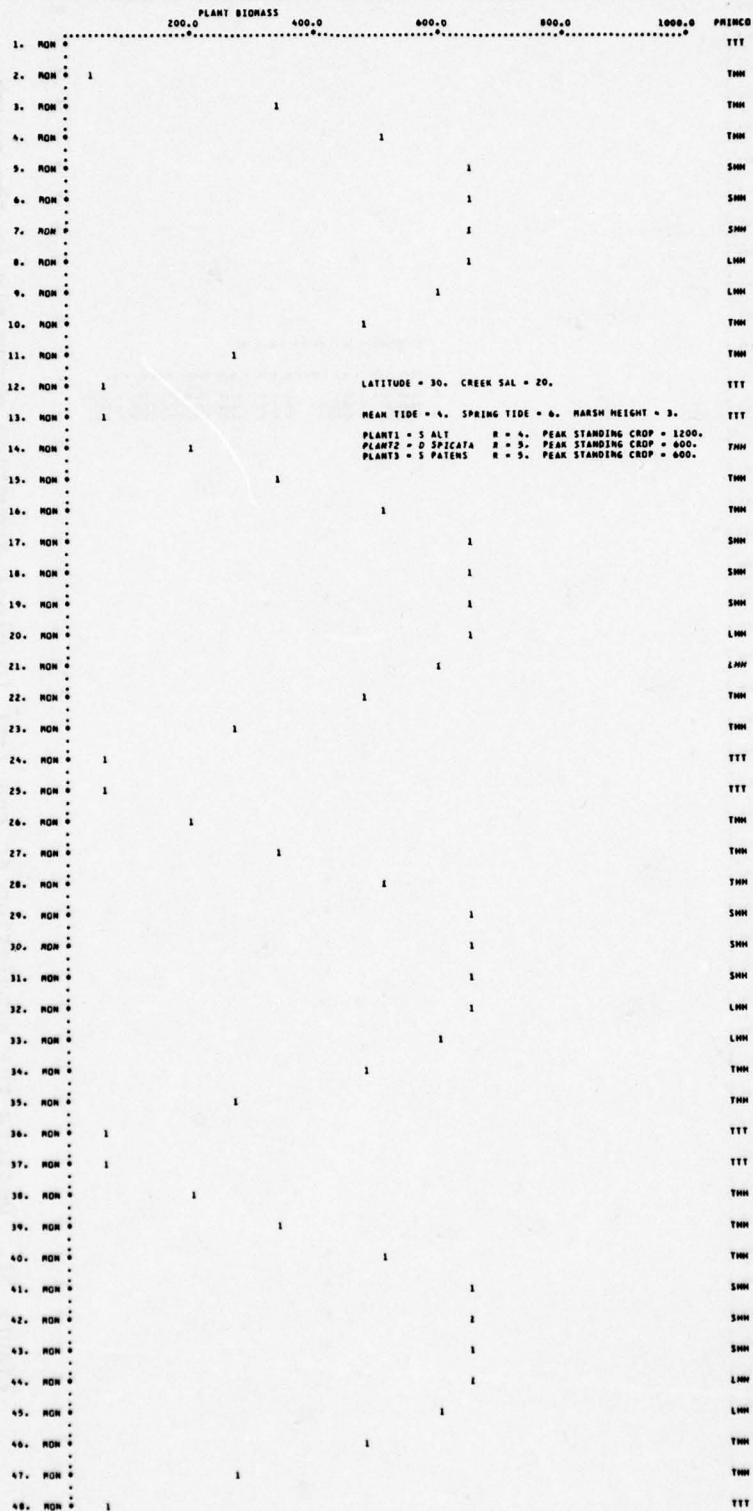
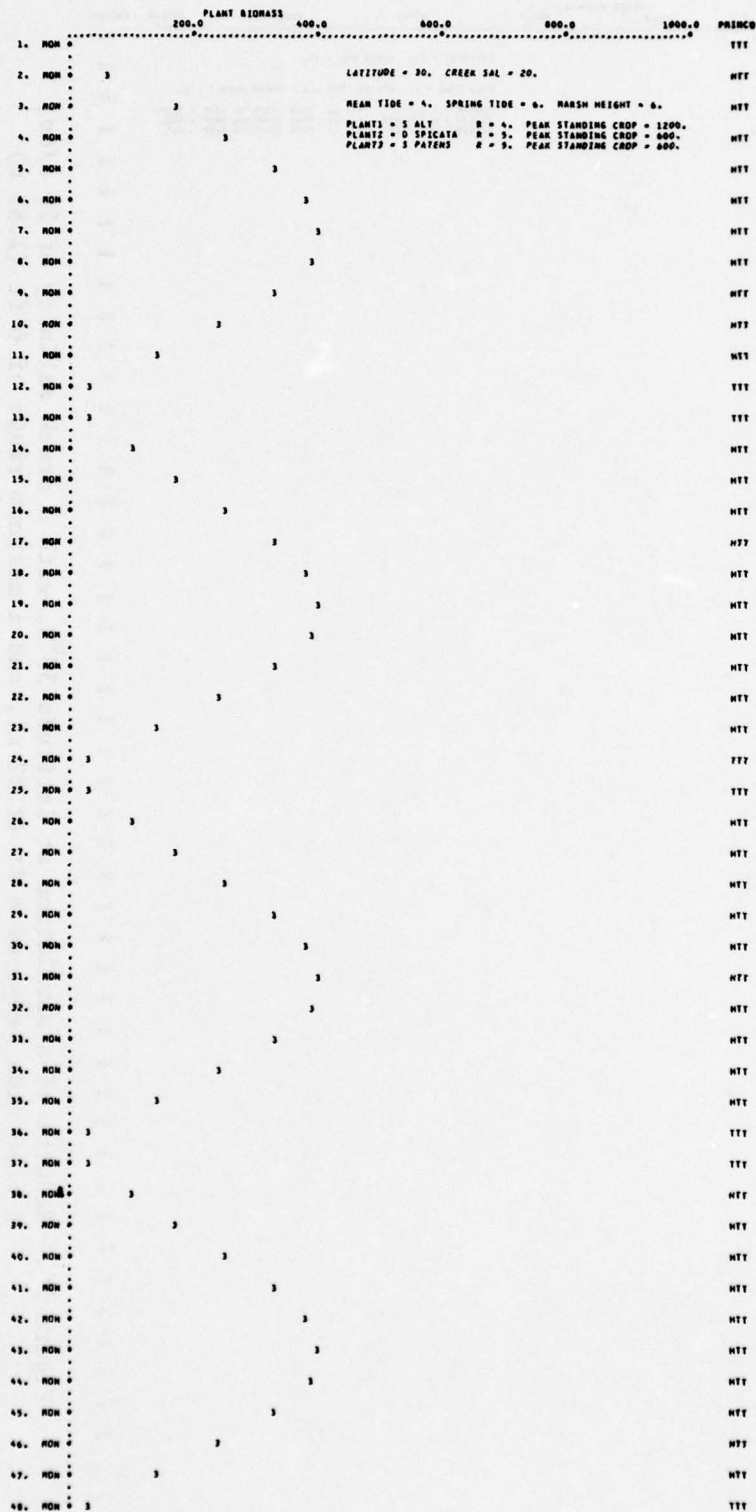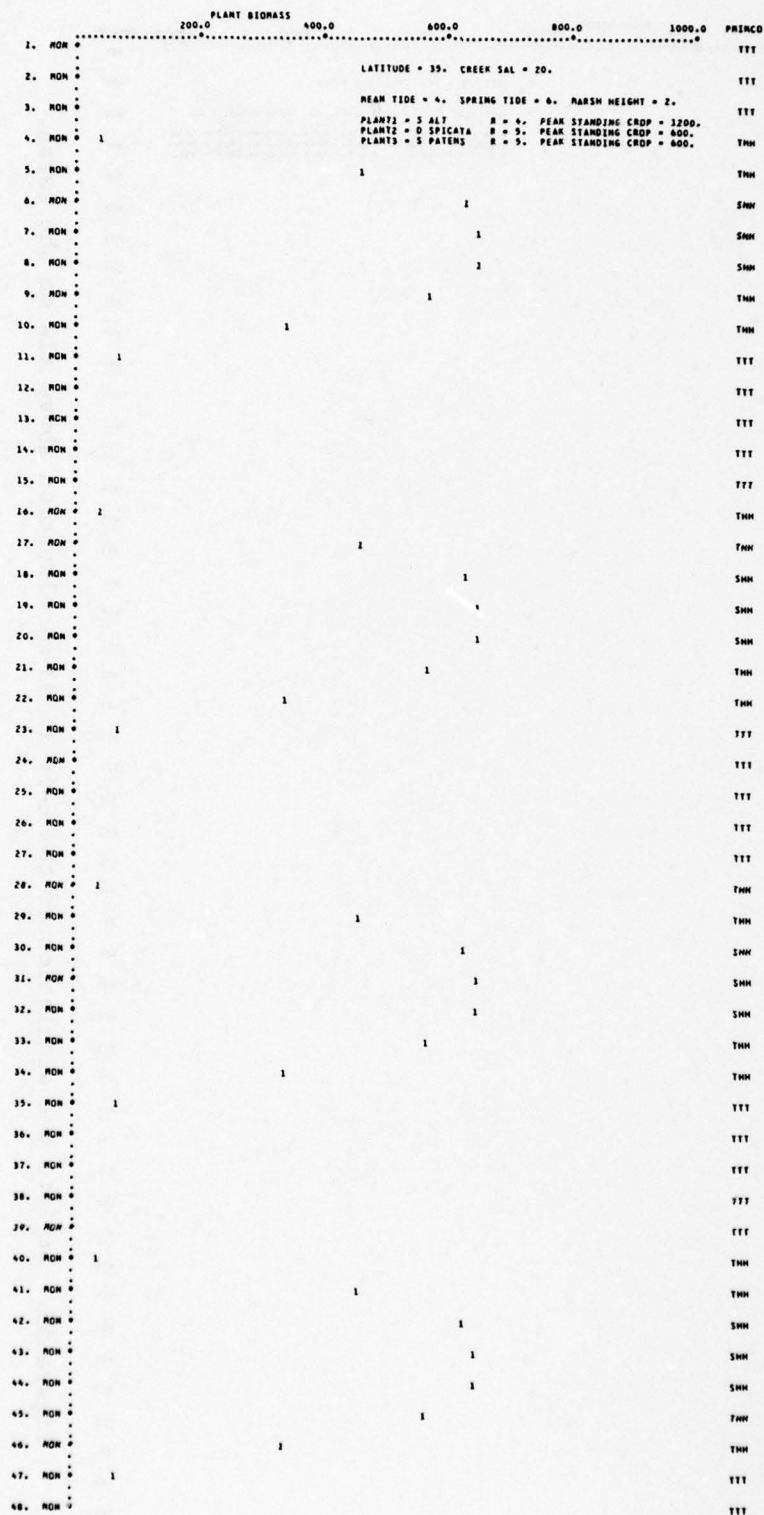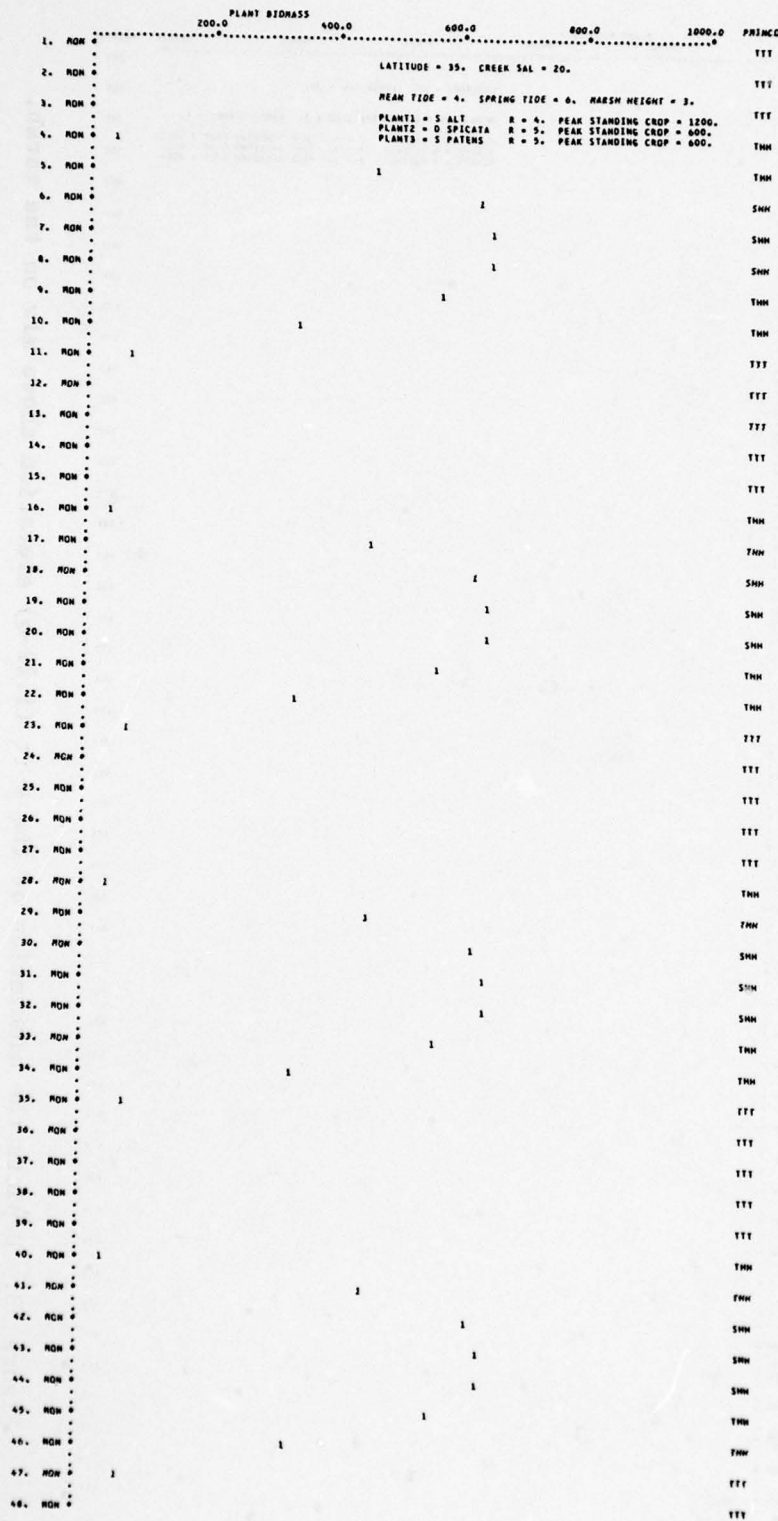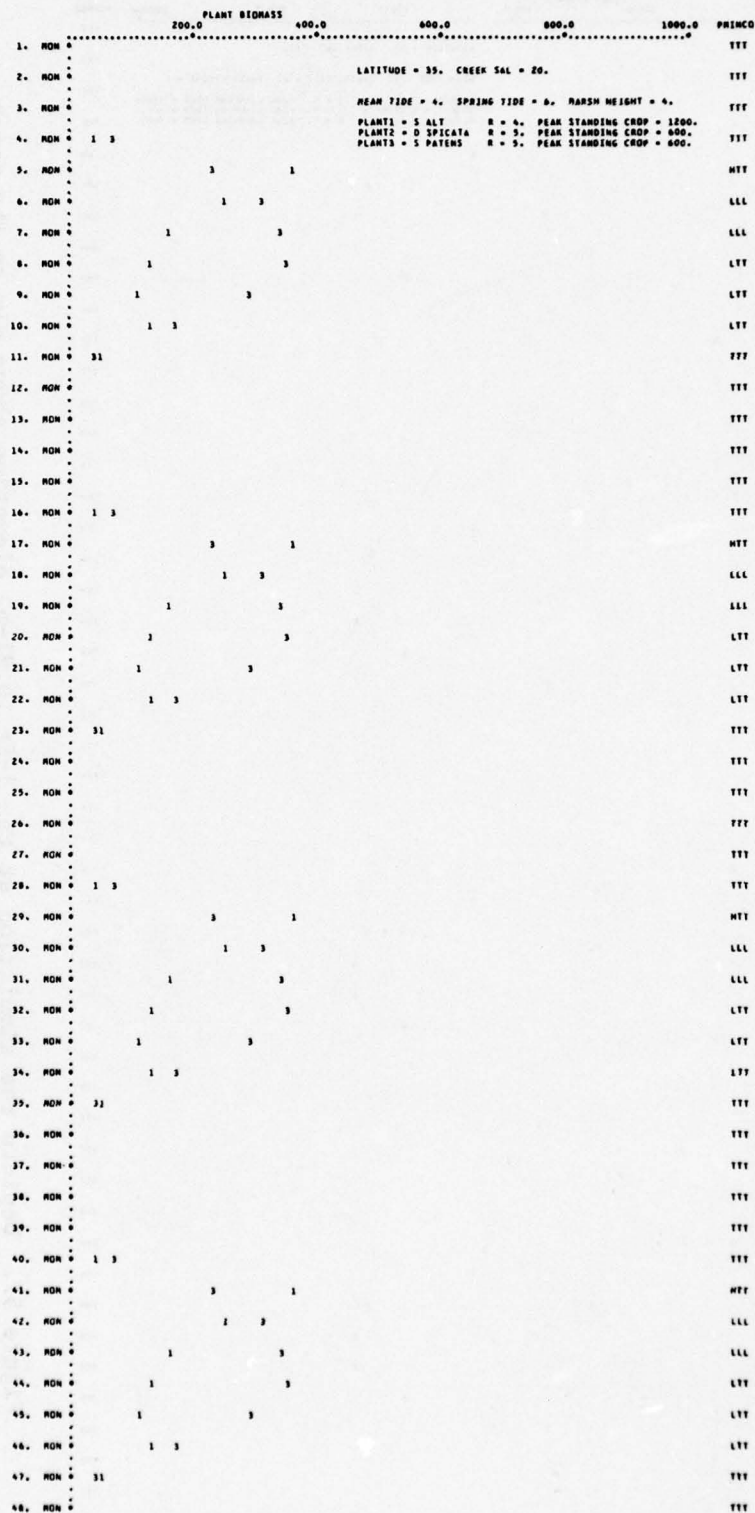Figure 57. Depicts the simulation at the 3-ft (0.91-m) elevation above mlw on the marsh.

147

PLANT BIOMASS

| | 200.0 | 400.0 | 600.0 | 800.0 | 1000.0 | PHINCO |

LATITUDE = 35. CREEK SAL = 20.

MEAN TIDE = 4. SPRING TIDE = 6. MARSH HEIGHT = 4.

PLANT1 = S ALT   R = 4. PEAK STANDING CROP = 1200.
PLANT2 = D SPICATA R = 5. PEAK STANDING CROP = 600.
PLANT3 = S PATENS   R = 5. PEAK STANDING CROP = 600.

```
 1. MON                                                                TTT
 2. MON                                                                TTT
 3. MON                                                                TTT
 4. MON    1 3                                                         TTT
 5. MON           3       1                                            MTT
 6. MON            1   3                                               LLL
 7. MON        1            3                                          LLL
 8. MON       1            3                                           LTT
 9. MON       1       3                                               LTT
10. MON        1 3                                                    LTT
11. MON    31                                                         TTT
12. MON                                                               TTT
13. MON                                                               TTT
14. MON                                                               TTT
15. MON                                                               TTT
16. MON    1 3                                                        TTT
17. MON           3       1                                           MTT
18. MON            1   3                                              LLL
19. MON        1           3                                         LLL
20. MON       3            3                                         LTT
21. MON        1           3                                        LTT
22. MON         1 3                                                  LTT
23. MON    31                                                        TTT
24. MON                                                              TTT
25. MON                                                              TTT
26. MON                                                              TTT
27. MON                                                              TTT
28. MON    1 3                                                       TTT
29. MON           3       1                                          MTT
30. MON            1 3                                               LLL
31. MON        1           3                                        LLL
32. MON       1            3                                        LTT
33. MON      1         3                                            LTT
34. MON        1 3                                                  LTT
35. MON    31                                                       TTT
36. MON                                                             TTT
37. MON                                                             TTT
38. MON                                                             TTT
39. MON                                                             TTT
40. MON    1 3                                                      TTT
41. MON           3       1                                         MTT
42. MON            1   3                                            LLL
43. MON        1           3                                       LLL
44. MON       1            3                                       LTT
45. MON        1         3                                         LTT
46. MON         1 3                                                LTT
47. MON    31                                                      TTT
48. MON                                                            TTT
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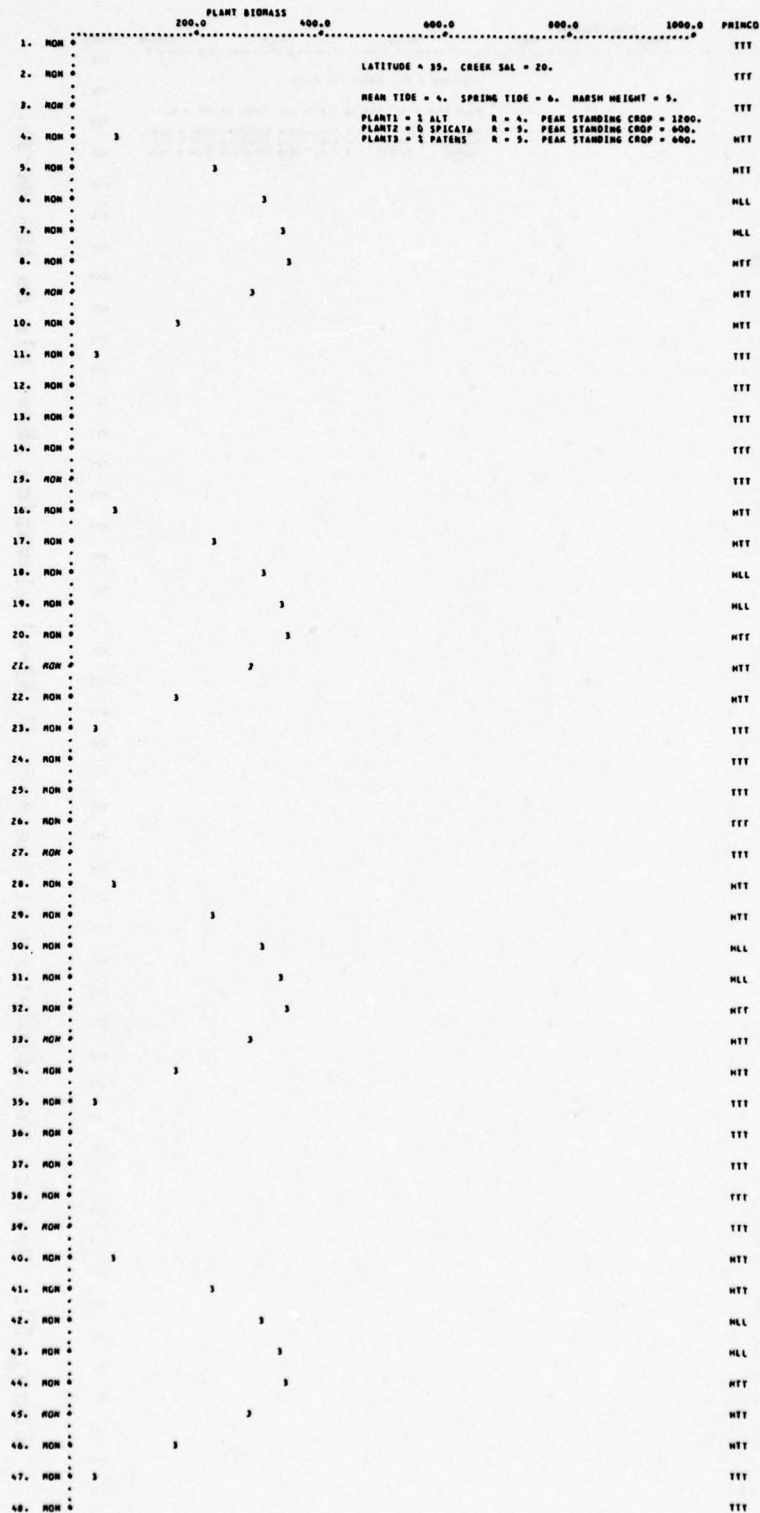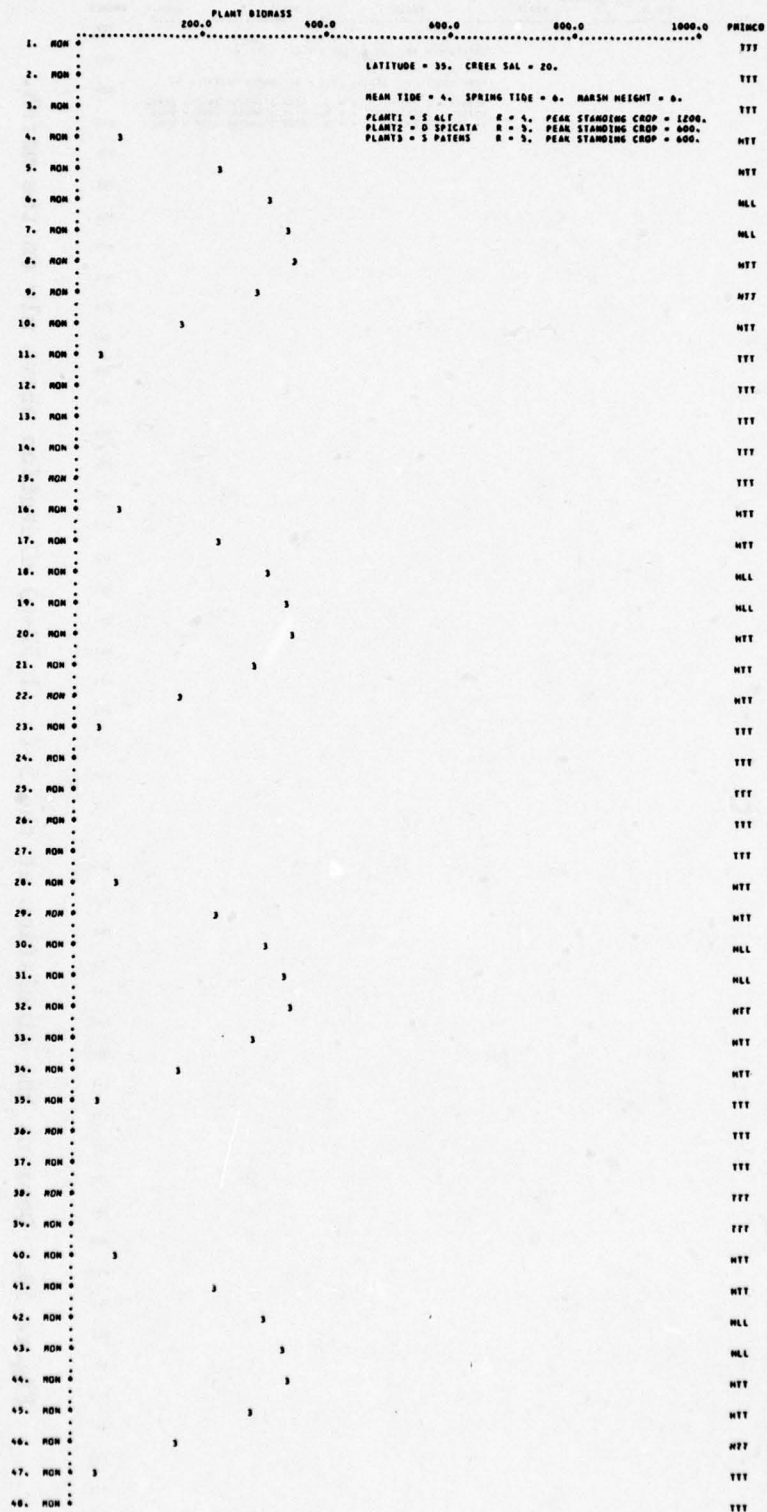Figure 58. Depicts the simulation at the 4-ft (1.22-m) elevation above mlw on the marsh.

148

PLANT BIOMASS

	200.0	400.0	600.0	800.0	1000.0	PHINCO
1. NON	. . . .					TTT

LATITUDE = 39. CREEK SAL = 20.

MEAN TIDE = 4. SPRING TIDE = 6. MARSH HEIGHT = 5.

PLANT1 = % ALT   R = 4. PEAK STANDING CROP = 1200.
PLANT2 = & SPICATA R = 5. PEAK STANDING CROP = 600.
PLANT3 = % PATENS   R = 5. PEAK STANDING CROP = 600.

Figure 59. Depicts the simulation at the 5-ft (1.52-m) elevation above mlw on the marsh.

149

PLANT BIOMASS

200.0   400.0   600.0   800.0   1000.0   PRIMCO

LATITUDE = 35.   CREEK SAL = 20.

MEAN TIDE = 4.   SPRING TIDE = 6.   MARSH HEIGHT = 6.

PLANT1 = S ALT   R = 4.   PEAK STANDING CROP = 1200.
PLANT2 = D SPICATA R = 3.   PEAK STANDING CROP = 600.
PLANT3 = S PATENS   R = 3.   PEAK STANDING CROP = 600.

Figure 60. Depicts the simulation at the 6-ft (1.83-m) elevation above mlw on the marsh.

marsh was located at a latitude of 35°N, and all other parameters were held constant. The location of species within the marsh with respect to tidal height was similar to that for the marsh at 30°N, but the temporal change of biomass and peak biomass varied considerably. In this more northerly area, the growing season would be shorter. This was reflected in a more rapid increase in biomass after growth is initiated. A slightly lower peak biomass level was found at this higher latitude, but because the growing season is shorter, the total area under the curve is considerably less than at 30°N. This relationship was found for all locations within the marsh.

142. The simulations used for illustration showed that radiation, temperature, and, particularly, tidal inundation controlled plant growth and plant location on the marsh surface. Salinity was seldom seen to be the limiting factor which generated the above results (Figures 50-60). This, however, may be largely due to an artifact of the parameterization of the model.

143. No model is any better than the data and constructional information used to generate the model. The model presented is of more utility than the results presented here. The results are limited by the parameterizations that were available when this model was originally constructed. However, the model was not so structured, and is limited only by the knowledge available when it is utilized. Therefore, all new data and theory generated that affects growth, distribution, and succession on a marsh may be incorporated in future simulations.

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PART VIII: SUMMARY AND CONCLUSIONS

144. At the outset of this project three parallel studies were designed to gain insight into the processes that determine plant growth and succession on estuarine salt marshes. The first was concerned with both the daily and seasonal ranges of marsh physicochemical parameters and the subsequent biotic responses within different vegetative zones. A series of marshes were visited and surveyed, but effort was concentrated on two intensive sites in Virginia.

145. The second study involved obtaining continuous records of several selected physical and chemical parameters from within the vegetation zone. This required the development of a continuous recording data monitoring system suitable for use in the estuarine system.

146. The third study of the project was the development of a simulation model of plant growth and succession on the marsh. The initial models were developed using information available in the literature on the functions of estuarine salt marshes. As the project progressed, information was added from field studies and contact with other scientists in the field.

147. Data from the first study were analyzed with correlation analysis of plant growth related to habitat condition and showed clearly that the growth of S. alterniflora exhibited a strong positive correspondence with elevation and tidal inundation at both major study sites. In addition, this plant demonstrated a negative correlation with soil salinity, while the standing crop was significantly correlated with iron availability.

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148. For S. patens and D. spicata, the measured responses to tides differed conspicuously. At one site where the high marsh was rarely flooded, the growth of neither species was closely related to inundation or elevation. At the other intensively studied site, which receives flooding during spring tides, there was a strong correlation of tide with S. patens (positive) and D. spicata (negative) growth. Wherever regular flooding takes place the growth of S. alterniflora and S. patens demonstrated a negative correlation with soil salinity while the more salt-tolerant D. spicata was positively correlated with salinity.

149. The fact that habitat factors are closely associated with both tide and plant growth wherever fairly regular inundation occurs suggests that inundation acts as a master variable influencing plant growth both directly and by controlling other features of the marsh habitat.

150. Conclusions drawn from the second study and the records of continuous field monitors tend to reinforce the concept of tidal inundation as the master variable for explaining plant distribution, especially in the region between the low tide marsh and the upper extent of spring high tides. The power spectrum analysis of continuous monitoring data from the marsh with an infrequently flooded high marsh provides a good example. The surface temperatures from the S. alterniflora zones showed the major power peak to be at 0.089 cycle/hour, which is the tidal frequency for this area, while in the higher S. patens - D. spicata zone, the frequency with the largest power

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component is that of nearly 1 cycle/day, corresponding to the input of solar radiation. The analyses of pH data further showed a large spike of the tidal frequency in the low S. alterniflora marsh, but not in the high marsh.

151. The third objective of this project, the development of a marsh successional model, was designed around the concept of species modules that depict the growth dynamics of S. alterniflora, S. patens, and D. spicata.

152. The species modules were combined into a point model that simulates the growth of each species on a particular square meter of marsh surface. Coupling of a series of point models enables simulation of plant growth both temporally and spatially across the marsh. The total marsh model is driven by four environmental variables: solar radiation, temperature, soil salinity, and tidal inundation. A special subprogram was developed to calculate the time of tidal inundation and number of tidal inundations per year at any height within a marsh.

153. Experimental simulations demonstrated that radiation, temperature, and, particularly, tidal inundation were responsible for controlling plant location and growth on the marsh surface. Salinity, at least in these preliminary runs, seldom appeared to be a limiting factor. In the final analysis, the model appears to have great utility for future research, but is limited at the moment by incomplete parameterizations.

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APPENDIX A: CONTINUOUS MONITORING SYSTEM

Concept

1. One severe limitation on the application of modern analytical techniques in estuarine ecology has been the inability to measure environmental variability in the field at a rapid rate. Most ecological measurements are made at infrequent intervals, and the time period between samples is relatively long. The experimental field data system described here was designed to monitor various physical and chemical parameters at a rapid rate and to monitor these parameters at several sites on the marsh simultaneously.

2. Because there was no commercially available system that would perform all of the functions desired, a unit was designed in a modularized fashion, combining commercially available components with sections whose designs were tailored to the project's needs. The objective of this segment of the study was to develop the capability to compare both long-term and short-term variations among different zones on the marsh. For this reason a system was designed and built that was able to monitor stations spread across several hundred meters of marsh surface. A similar data recording system was constructed by several other members of the University of Virginia Department of Environmental Sciences for monitoring eutrophication in rivers. The final report of this study (Kelly et al., 1975) describes the theory and circuitry in great detail

A-1

Configuration

3. Figure A-1 illustrates the overall configuration of the system as deployed in the field, and Figure A-2 depicts the contents of one submersible amplifier unit with sensors and power supply. The system consisted of the following major components:

    <u>a</u>. Sensors to measure the magnitude of the described parameter.

    <u>b</u>. Cable leads to connect the sensors to the electronic amplifiers.

    <u>c</u>. Signal amplifiers with power sources to amplify the measured signal and connect it to voltage compatible with the data recorders.

    <u>d</u>. Waterproof housing to shield the amplifiers and batteries.

    <u>e</u>. Connecting cables to transmit the amplified signal to the data recorders.

    <u>f</u>. Junction or distribution boxes to allow the selection of the various parameters that are to be recorded at a particular time.

    <u>g</u>. Digital data recorders to record the signals.

    <u>h</u>. Waterproof housing to shield the recorders.

Field Sensors

4. Temperature was measured electronically by a twin bead thermistor and an accompanying amplifier. A Fenwal GB 34PMG2 Iso-curve glass head thermistor was used. The variable resistance of the thermistor is measured by the amplifier and the signal converted to a 0.0 to 1.0 v-d.c. output. The amplifier may be adjusted so that the one valid output range corresponds to a variety of temperature ranges. For
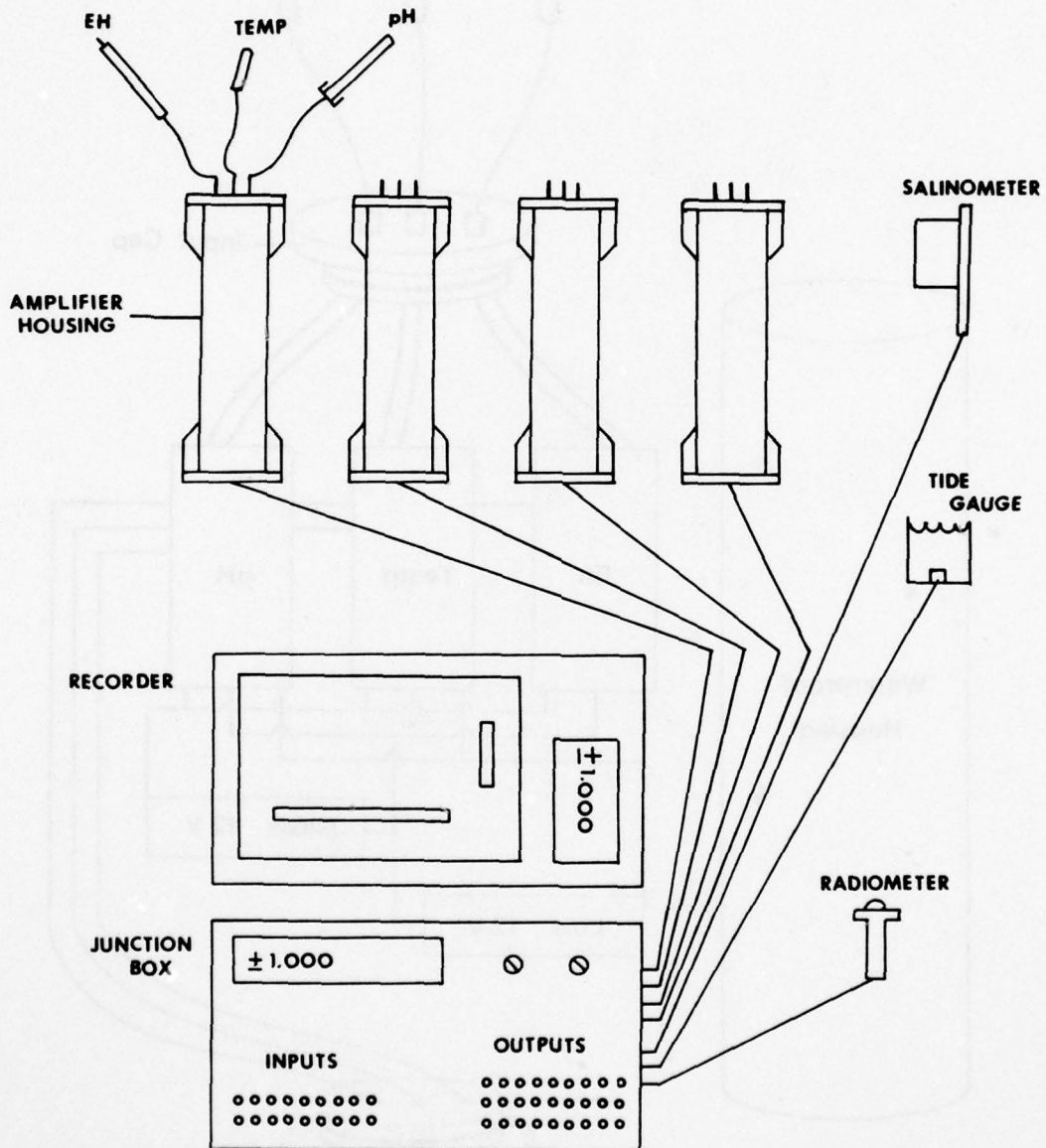
Figure A-1. General configuration of the data monitoring system.
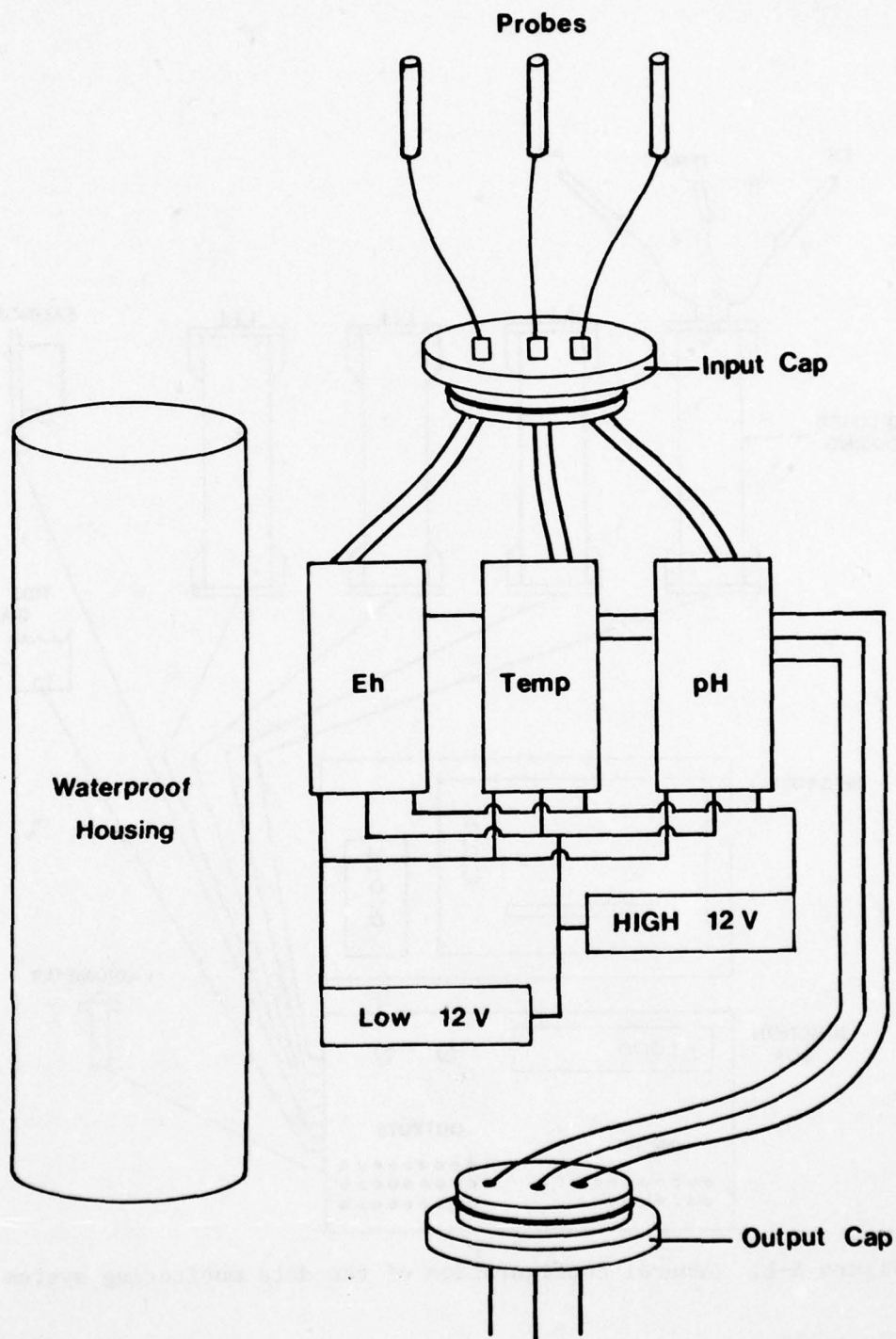
Figure A-2. Typical configuration of one submersible housing unit.

the uses of this project the range selected was 0-40^{o}C. The thermistor
is soldered to a lead wire, and the thermistor and solder joint are
molded into a 10-cm length of clear polymer plastic using Scotchcast
electrical potting compound to provide electrical insulation and struc-
tural strength. The resulting unit is exceptionally rugged and resists
damage from general field use. Accuracy is approximately ± 0.1^{o}C.
pH

5. Combination pH/reference electrodes have been found to give
satisfactory performance under the extreme conditions of use they
would experience in this project. Electrodes must withstand submergence
for extended periods of time in seawater, and must be able to function
in sediments that are abrasive and frequently anaerobic.

6. Initially the Thomas 4094-510 sheathed-in-glass combination
probe was used. This gave satisfactory performance, but was vulnerable
to breakage. Because it is not sealed, it required modification for
this field use. Furthermore, it has to be refilled periodically.

7. The electrode generally used was the Sensorex Model S300C,
which is a combination electrode with a completely sealed construction.
This is permanently filled with a saturated gell KCl, and is contained
in a high impact polymer case. These electrodes may be used as pur-
chased for short times, if great care is taken. For heavy or pro-
longed use it proved necessary to further protect the cable lead and
the joint where the cable lead enters the probe. This was done by
threading the lead wire through a length of 1/8-in. Tygon tubing and
sealing the tubing to the head of the probe with household caulking
compound. The joint was then securely wrapped with electrical tape.

A-5

8. The pH amplifier was a solid state, expanded scale pH meter with an Analog Devices model 173J Isolation Amplifier to reduce current leakage problems from the electrodes and errors due to ground loops in the highly conductive medium where the system must function. The pH amplifier gives an output of 0.0 to 1.0 v-d.c., which is normally equivalent to pH 4.0 to 10.0 ± 0.1, although this range is adjustable.

Eh

9. The oxidation-reduction potential or Eh system utilizes the same expanded scale pH amplifier as the pH sensor, but as the signal is several orders of magnitude greater than across a pH sensor pair, the isolation amplifier is omitted at present. The platinum electrode is made by soldering a 22 gauge platinum wire about 405 cm long into a 12-cm brazing rod. This unit is sealed into a 20-cm pyrex tube with polyester resin. For a reference, this unit utilizes a Sensorex reference electrode or shares the reference half of the combination pH electrode. The amplifier gives 0.0 to 1.0 v-d.c. output for Eh values in the range of ± 400 millivolts. This unit, however, has been the source of major problems: current leakages that cause erratic Eh recordings and also interfere with the pH readings. Another problem is that there are few standards with which to calibrate the units. The most commonly used is Zobell's solution with an Eh of +430 millivolts at 25^{o}C.

Salinity

10. Salinity of the water in tidal creeks was measured by an Instro Company model 300 inductance salinometer. Salinity was determined by an inductive-conductive measurement that was internally compensated for temperature effects and linearized. The unit

required a nominal 9 to 15 v-d.c. input and gave an output of 0.0 to 1.0 v-d.c. which corresponded to 0 to 40 ppt.

Solar radiation

11. Incident solar radiation was measured by an LI-200 SR Pyranometer (Lamda Instrument Corporation) that consisted of a silicon solar cell mounted beneath a diffusing surface and designed to give a cosine response. As the relative spectral response is not constant over the full range of the solar spectrum, the sensor should be used only in the open air and not under plant canopies or artificial lights. This instrument measures radiation directly in watts per square meter, giving total energy input. Absolute accuracy is ± 5 percent when calibrated against an Epply Pyranometer under natural daylight and clear conditions.

Tide height

12. The tidal level in the nearby marsh was measured by a Sensotec Model FJE pressure transducer, an absolute pressure unit with a reference of 14.3 psi sealed in the reference chamber. It possessed built-in electronics, received ± 12 v-d.c. inputs, and gave an output of 0.0 to 1.0 v-d.c. corresponding to 0.0 to 6.09 m of water pressure with an accuracy of ± 0.1 percent of full scale.

Signal Amplifiers and Housings

13. The sensors for temperature, pH, Eh, and solar radiation were connected via waterproof cables and connectors to housing which contained signal conditioning amplifiers for the sensors. Because of the extremely low voltages and current across the sensors, especially the

pH probe, there was a limitation in the length of the lead wire between the sensors and amplifiers. In the field unit, this length was kept below 3.5 m.

14. The signal conditioning amplifiers required ± 12 v-d.c. that was supplied by battery packs. The battery packs and amplifiers were housed in pressureproof housings. These housings were milled from 10.6-cm i.d. PVC tubing, and were closed with O-ring sealed end PVC caps. The battery packs used sixteen 15 v-d.c. transistor batteries (D cells) each; one pack powered a set of three or four amplifiers clustered together in each tube for over two weeks. An alternate method to supply power would be to run power cables from a central battery source to each tube and to the data recorder. This option was tried initially, but was discarded due to problems with current leaks and ground loops between the sensors, recorders, and amplifiers.

15. From the amplifier tubes, the signals were fed back through waterproof cables and connectors to a junction box.

16. Certain instruments, such as the salinometer, current meter, and tide gauge, were protected by their own self-contained housings, and linked directly into the junction box.

Junction Box

17. All field sensors were connected to a junction or distribution box. This was currently capable of receiving the input from 40 field sensors. A Fluke model 8000 digital multimeter was utilized as a readout device, and all of the 40 inputs could be monitored on the

digital meter by dialing the appropriate input channel. A patch panel was provided on the front of the junction box, and any of the 40 input channels could be patched into the 16 inputs to the tape recorder for continuous monitoring. Thus, 16 channels could be monitored continuously by the recorder, or 40 channels of data might be monitored intermittently by use of the digital output unit. When using this device manually, however, coding was necessary as the sensor amplifiers read out as 0.0 to 1.0 v-d.c. outputs and not as scaled values. As a result, conversion curves of nomographs were used to determine the actual value of the parameter being measured.

Recorder

18. The data were transmitted from the junction box through moistureproof cables and couplings to the recorder unit. The recorder was a Metrodata Dl-616 data logger coupled with a DR-99 digital readout. The data logger recorded on a 6.35-mm endless loop tape cartridge in serial format. The analog input was converted to digital format for filing on the tape. Recording times could be varied from continuous (approximately 2.5 full 16 channel scans per second) to one scan each 73 minutes via a switch from a quartz clock. The unit was capable of operating from either a 115 Hz or 12 v-d.c. source.

19. Although these units were rather sophisticated, the field record was quite acceptable. The only consistent stoppages occurred when the temperature dropped below freezing. Modifications were required to decrease the sensitivity of the end-of-tape markers; aluminum

foil markers were placed to keep the recorder from overrunning the end of the tape. A photocell sensed the reflected light from a small light source, but in field use the intense natural light, even when units were shielded, caused premature shut-off.

20. The major problem encountered with the recorder data, as opposed to the actual recording, was with the retrieval of the data. During the recording of field data, especially if 12 v-d.c. was used as the power source, the recorders may occasionally have skipped one or more of the 16 channels that were being recorded. This presented few difficulties if the location of the lost channels were known. In practice, this was one of the several drawbacks of the entire continuous recording system.

21. The format of the data recorded on the field units was filed in a unique way that was not compatible with the normal data processing computer. For this reason, it was transcribed from 6.35-mm data tape to 12.7-mm computer tape in compatible format. This was done by using a metrodata tape transcriber.

Data Processing

22. After transcription, the field data were processed to convert the raw millivolt readings from the amplifiers into the absolute values for each of the parameters.

23. The processing of the recorded data proceeded via several steps. The cartridge tape records retrieved from the field were reformatted and transcribed onto industrial standard seven-track magnetic tapes using a Metrodata model 625 tape reader driving a Digi-Data

recorder. A block length of 960 characters was used as optimal for input to the CDC 6400 computer used in this study. This taped information was then used as input into a series of computer programs resulting in diurnal curves of radiation, tide, pH, and temperature.

24. The first program accessed was TRANSCRIBE (see Kelly et al., 1975, for complete description), which converted the recorded input voltages on the seven track tape into decimal equivalents. Simultaneously, it checked for outlier data points and errors in recording. The output from this program was written onto a permanent master tape that could be accessed at some future date.

25. At this stage a program, PROCESS, was utilized to convert the millivolt readings into absolute values (see Kelly et al., 1975, for detailed description). This conversion utilized the output tape produced by TRANSCRIBE in addition to field calibration information. Within the program, the continuously monitored information was averaged for a period of time specified by the operator and then converted to absolute values via a series of mathematical formulations. This information could be either printed, punched onto cards, or written onto another tape or disc file. For purposes of visual display and analysis, the punched card output was used as input to a plot routine, which plotted the radiation, tide, temperature, and pH as a function of time. This information could be displayed in a variety of formats that included fixed and variable scales for the y-axis as well as plotting all environmental parameters at one station and/or comparing parameters between stations.

APPENDIX C: SURVEY SITES

1. Plant and sediment surveys were conducted at a variety of sites along the eastern seaboard, from New Jersey to Georgia, to attempt to determine if the pattern shown by the zonation of the marsh plants was reflected by certain constituents within the sediments. Most of these sites were visited only once--on extended survey trips-- although a subsequent trip was conducted to several of the sites in order to collect a biomass estimate from the end of the growing season. Many of the sites were visited by students and personnel only parti- ally connected with this study, and as a result, the data sets are not uniform.

2. The name and computer abbreviation of the survey sites are listed in Table C-1 and the location of the sites is shown in Figure C-1. The objective at these sites was not the creation of detailed vegeta- tion maps and fine scale resolution of the changes in chemical and bio- tic parameters, but the general depiction of trends in certain chemi- cal constituents of the sediments, and their relation to changes in the dominant vegetative species.

3. At the survey sites, sampling stations were located on a transect that extended from the lowest elevation colonized by Spartina alterniflora, through the S. alterniflora zone into the high marsh where this pattern existed. The stations with the lowest numbers were the lowest areas colonized by S. alterniflora and the highest numbers

were generally the uppermost region of the high marsh. (Exceptions to this are Taskinas Marsh and Bennett's Marsh, but these are described in detail.) Transect lengths varied greatly but these, unfortunately, were not always recorded. Vegetation samples and sediment cores were attempted at each station. Single or duplicate samples of live standing crop were taken; however, some samples were lost. Quadrat size was varied according to plant type and density; $0.1m^2$ quadrat samples were harvested in the $\underline{S}.$ $\underline{alterniflora}$ zone and 0.04 m^2 samples were taken where the much denser $\underline{S}.$ $\underline{patens}$ or $\underline{D}.$ $\underline{spicata}$ predominated. These samples were sealed in plastic bags for transporting to the laboratory for counting and weighing. Table C-2 gives the computer abbreviations for the plant data.

4. Sediment cores were taken with either a 7.6-cm (3-inch) internal diameter P.V.C. corer or a 6.35-cm (3.5-inch i.d.) brass core tube. These were extruded in the field, wrapped securely in plastic bags, and frozen with dry ice for transportation to the laboratory.

5. For certain samples, the pH and oxidation-reduction potential (EH) of the sediment were measured immediately upon extrusion of the core. pH was measured using a Sensorex S 200 c combination pH electrode, and an Orion model 401 portable pH meter. Eh was measured using the reference half of the combination pH electrode and a Thomas 4096-D20 platinum electrode.

6. Cores were stored at $-15^{o}C$ prior to lab analysis. After thawing for 12-18 hours at room temperature, each core was divided into 10-cm sections. A subsample weighing 12.5 g (wet weight) was

cut from each of these sections on a longitudinal strip. These sub-
samples, representing the three cores obtained from the same sample
zone and depth range (a total of 37.5 g of sediment), were consolidated
with 150 ml of extractant solution (0.025 N HCl + 0.01 H_2SO_4) (Nelson
et al., 1953) and homogenized for 30 seconds at high speed in a stain-
less Waring blender. The resulting solution was filtered through
Whatman #42 filter paper and collected in plastic sample bottles.
Several drops of chloroform were added to each sample bottle to inhi-
bit bacterial activity. Filtered samples were frozen until analysis.
Cores from the survey sites were treated similarly, but only one core
was utilized per analysis.

7. Subsamples from all three cores representing a given sample
zone were consolidated, as above. Consolidated subsamples were dried
in a warming oven for 48 hours at 100°C. Dried samples were cooled
and reweighed, then pulverized with mortar and pestle. Subsamples of
approximately one gram were transferred to crucibles and weighed
within ± 0.0002 g on a Sartorius analytical balance. The samples were
then ashed in a muffle furnace for 12 hours at 550°C and were
reweighed after cooling in a desiccator. Percent organic matter was
determined by weight loss during ashing.

8. In the data section that follows, the following units are
used: biomass (grams dry weight/m^2), stem height (cm). All chemical
values are in parts per million (p.p.m.) and the day in the Julian
day of the year.
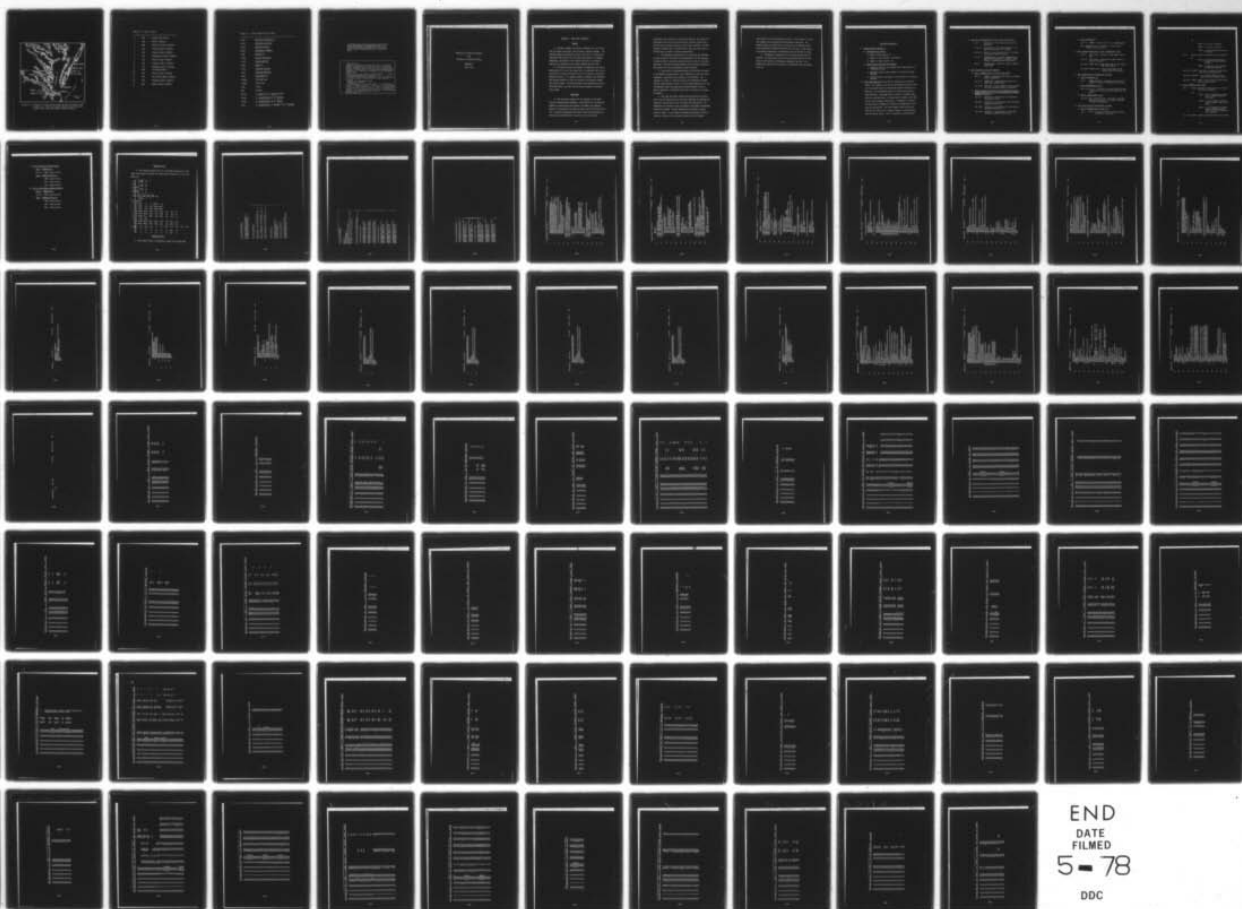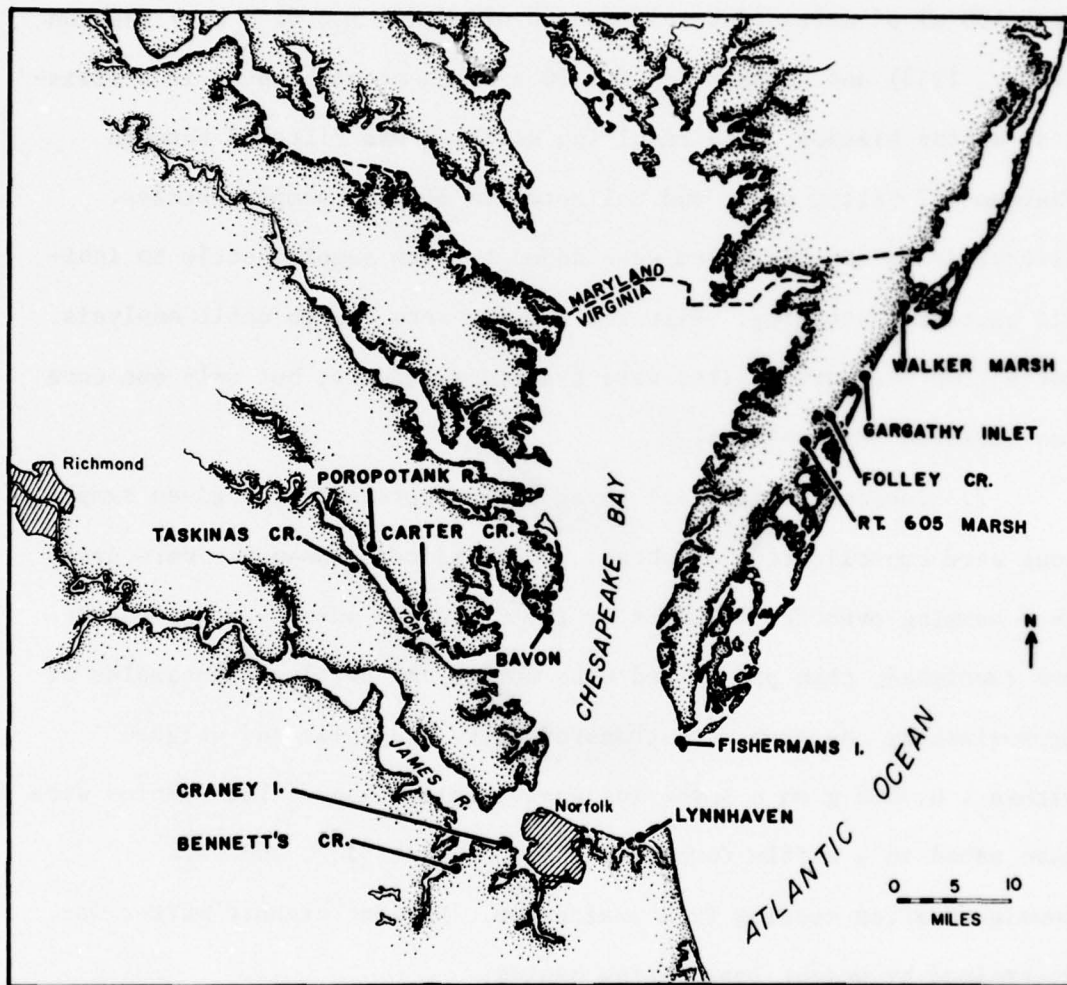
Figure C-1. Location of survey sites along the central eastern coast
of the U. S. The two sites not shown on the figure are
Avalon, New Jersey, and Sapelo Island, Georgia.

Table C-1. List of Sites

1	AVA	Avalon, New Jersey
2	BAV	Bavon, Virginia
3	BEN	Bennett's Creek, Virginia
4	CAR	Carters Creek, Virginia
5	CRA	Craney Island, Virginia
6	FIS	Fishermans Island, Virginia
7	FOL	Folley creek, Virginia
8	GAR	Gargathy Inlet, Virginia
9	LYN	Lynnhaven Inlet, Virginia
10	POR	*Poropotank River*
11	SAP	Sapelo Island, Georgia
12	605	Route 605 Bridge, Virginia
13	TAS	Taskinas Creek, Virginia
14	WAL	Walker Marsh, Virginia

Table C-2. Plant Identification Codes

S.ALT	_Spartina alterniflora_
D.SPI	_Distichlis spicata_
S.PAT	_Spartina patens_
PHRAG	_Phragmites communis_
SCIR	_Scirpus_ sp.
J.ROM	_Juncus romerianus_
J.GER	_Juncus gerardi_
TYPHA	_Typha_ sp.
S.EUR	_Spartina europea_
S.BIG	_Spartina Bigelowi_
SALIC	_Salicornia_ sp.
S.DEAD	Standing dead
T.DEAD	Total dead
LITT	Litter
UNK	Unknown
SP-DS	_S. patens_ and _D. spicata_ mixed
SA-DS	_S. alterniflora_ and _D. spicata_
SA-SP	_S. alterniflora_ and _S. patens_
P-DS	_S. alterniflora_, _S. patens_, and _D. spicata_

In accordance with letter from DAEN-RDC, DAEN-ASI dated
22 July 1977, Subject: Facsimile Catalog Cards for
Laboratory Technical Publications, a facsimile catalog
card in Library of Congress MARC format is reproduced
below.

Modeling of Ecological Succession

And

Production in Estuarine Marshes

APPENDIX B

TR D -77-35

APPENDIX B: MODEL USER INFORMATION

General

1. The model, MARSH1, was written in FORTRAN IV as this is the most universally used higher level scientific computer language. The original design and implementation were carried out on a Control Data Corporation 6400 machine, but the program was written to be machine-independent, and machine or CDC software functions or conventions which are not available on other brand computers were not used.

2. The model structure was designed for versatility and ease of modification of the input and output data. Of particular note is the relative ease of using the model from any of a variety of interactive keyboard terminals. If a computer system is available with sufficient bulk storage capacity to allow the storage of the program, terminal use is quite simple. The output routines allow specification of 80 or 132 column output, and other plotted output variables are automatically scaled.

Data Input

3. The input data necessary for the execution of the model falls into three general categories: site-specific data includes the numbers of stations along the transect, the number and species of plants to be included in the parameterization, and the latitude of the site. The model parameterization values include such information as the type of growth algorithm, the time step for the numerical

integration, and intervals for printing and plotting. The plant parameterization section includes plant specific intrinsic growth rates and the curves of species response to the driving variables. The most frequently changed cards, the site-specific data, are placed first in the data deck, in order to facilitate manipulation.

4. The parameters associated with the input data are explained in the next section and should be self-explanatory with the exception of those related to the species parameterization curves and the growth algorithms. The species parameterization curves represent response of the plants to the four environmental forcing functions.

5. The x-axis of the parameterization curve reflects the value of the specific forcing function (e.g. temperatu.e), while the y-axis represents a normalized growth response to this variable. The response of a plant to a specific level of an environmental forcing function ranges between 0.0 and 1.0; if the plant response is 0.0, the environmental factor has completely curtailed metabolic activity, while a response of 1.0 indicates the level of the factor is optimum for growth.

6. The other data input variable which may require clarification is the one associated with the growth algorithm; the mathematical method for calculating the level of biomass for each species. Two algorithms are available within this program, the logistic and maximum productivity methods. Several assumptions are inherent in using either of these. In the logistic formulation productivity is determined as a function of the intrinsic growth rate, the limiting

coefficients, and the contemporaneous biomass. Also included is a negative feedback term associated with environmental inhibition. The maximum productivity algorithm is the product of the limiting coefficient multiplied by maximum productivity per unit time. Either method is applicable depending on the assumptions the user desires to accept.

7. Following is a description of data input and data card preparation. The user should first have read carefully Part VII of this report as this section is designed to supplement that Part. The example data used here will reproduce the simulations shown in Figures 50 to 55.

Data Card Preparation

I. General program information

    A. Limitations per problem

        1. Number of plant species < 5

        2. Number of time intervals < 500 (months)

        3. Number of sites in marsh < 10

    B. Output options available from program

        1. Graphical output of the standing crop of each species, as a function of time.

        2. Graphical output of plant growth, as a function of space and time.

        3. Printed output of the growth of each species, as a function of time.

II. Data Card Preparation (each data set contains one or more data cards). The columns to the left of each parameter discussed indicate the location where the information should be placed on the data card. All information typed on the data cards should be right-justified. This means that if there are 5 columns designated for a variable and it is represented by 2 digits, place them in the 4 and 5 columns, respectively. In addition, a listing of the data format in FORTRAN is included at the beginning of each data card description. The actual numbers typed on the input cards may be either real or integer (integer - no decimal point, real has decimal point). This is specified for each variable.

B-4

A. **Set 1 (1 card) FORMAT(4X, I1. 2X, I3, 1X, F4.2, 4X, I1).**

  col 5   NUM(integer) = the number of species to be simulated.

  col 8-10   IMAX(integer) = the maximum number of time units per simulation (i.e. months).

  col 12-15   DT(real) = the time interval for the integration routine (between 0 and 1).

  col 20   METHOD(integer) = variable designating the productivity algorithm, 1 = logistic formulation, 2 = maximum productivity method.

  col 25   NCASE(integer) = number of cases of separate simulations.

B. **Set 2 (3 card set for each species)**

  1. **Card 1 FORMAT(1X, F4.1, 5X, F5.0, 1X, F4.0)**

     col 2-5   R(real) = intrinsic growth rate for the plant under consideration.

     col 11-15   PEAKB(real) = peak standing crop for the plant under consideration.

     col 17-20   VAL(real) = initial biomass to start simulation for the species under consideration.

  2. **Card 2 (scaling factor (0.0 to 1.0) uniformly scales up or down response of plant to an environmental parameter) FORMAT(4 (2X, F3.1))**

     col 3-5   LST(real) = scaling factor for light parameterization curve.

     col 8-10   TSF(real) = a scaling factor for temperature parameterization curve.

     col 13-15   SSF(real) = scaling factor for the salinity parameterization curve.

     col 18-20   HSF(real) = scaling factor for the tidal inundation parameterization curve.

3. Card 3 FORMAT(PA10)

   col 1-10   ISPECIE = species name (i.e. S. alterniflora).

   Note: Remember that this sequence of three cards is repeated for each species.

C. Set 3 (general marsh data, 1 card) FORMAT(4(1X, F4.0))

   col 2-5   ZLAT (real) = latitude of marsh under simulation.

   col 7-10   XSAL (real) = average marsh creek salinity in parts per thousand.

   col 12-15   RANGE (real) = mean tidal range in feet (source, NOAA tidal tables).

   col 16-20   SPRING (real) = spring tidal range in feet (source, NOAA tidal tables).

D. Set 4 (general site A information, 3 cards)

   1. Card 1 FORMAT(4X, I1)

      col 5   NUMHT (integer) = the number of sites along a transect for which a simulation is to be run.

   2. Card 2 FORMAT(10(1X, F4.1))

      col 5, 10, 15 etc. HT (real) = the actual height of each site along the transect in feet above mean low water.

   3. Card 3 FORMAT(10(1X, F5.3))

      col 2-6, 8-12, 14-18, 20-24 etc. DEP (real) = the sediment deposition rate for each site along the transect in feet/month.

E. Set 5 (print and plot information, 2 cards)

   1. Card 1 FORMAT(2(4X,I1), 3(3X, I2))

      col 5   IFLAG = parameter specifying whether printing or plotting is desired.

B-6

If:

NFLAG = 0, plotting is desired.

IFLAG = 1, printing is desired.

IFLAG = 2, both printing and plotting
is desired.

col 10   NFLAG = parameter specifying style of plotting

If:

NFLAG = 0, plotting species growth
through time at a particular
station.

NFLAG = 1, plotting a species growth
through space and time.

col 14-15 IPLOTDT = plot interval (number of time inter-
vals between plotted points).

col 19-20 IRPRINDT = print interval (number of time
intervals between printed points).

col 24-25 INTER = number of blank spaces between plotted
data on graphic output.

2. **Card 2 FORMAT(4X,I1,5X, F5.0)**

col 5   KFLAG = parameter designating how the range on
the y-axis is computed.

If:

KFLAG = 0, all variables are plotted
using a combined range for
the y-axis.

KFLAG = 1, each variable is plotted
using a separate range on the
y-axis.

KFLAG = 2, all variables are plotted
using a combined range for
the y-axis which is specified
by the operator.

col 11-15 QMAX = operator specified range for the y-axis.

B-7

F. <u>Set 6 (output plot width, 1 card)</u>

   <u>Card 1</u>   FORMAT(4X,I1)

   col 5   MFLAG = parameter specifying width of the out-
                        put graph.

             If:
                   MFLAG = 0, 100 characters (used for
                              large printer output).

                   MFLAG = 1, 80 characters (used for
                              teletype terminal output).

G. <u>Set 7 (1 card)</u>   FORMAT(5A10)

   col 1-50   NAME = legend of the y-axis.

H. <u>Set 8 (data input related to the solar radiation parameteriza-
   tion curve, 2 or more cards for each specie</u>:

   The parameterization curve is composed of a series of
   line segments ordered from left to right.

   example:
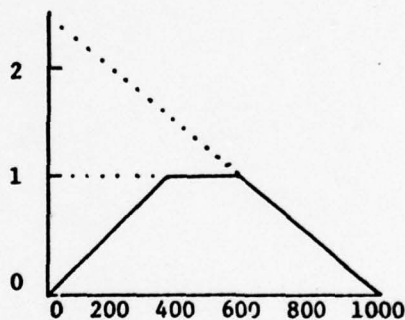
   <u>Card 1</u>.   FORMAT(4X,I2)

   col 5-6   NUML = number of line segments in the paramet-
                       erization curve. In the above example
                       NUML = 3.

Card 2-n. FORMAT(11(1X,F6.2))

The three variables to the right are typed sequentially on
as many data cards as necessary. Each data point within
each variable occupies 6 spaces (right justified) and is
separated by 1 column.

> CLEN = the endpoint of each line segment (i.e.
> value on x-axis corresponding to end of
> line segment). In the example CLEN =
> 400.0, 600.0, 1000.0.

> LL1 = y-axis intercept of each line segment.
> LL1 = 0.0, 1.0, 2.5 for each respective
> line segment in the above example. Note
> that the y-intercept of segment 3 is 2.5
> even though the parameterization curve
> never reaches this value.

> LL2 = slope of each line segment. In this
> example LL2 = 1.0, 0.0, -1.0.

In this example the 2nd card would appear as follows 400.0,
600.0, 1000.0, 0.0, 1.0 2.5, 1.0, 0.0, -1.0. The paramet-
erization curves may have any number of segments. If the
curves require more spaces than are available on one card,
simply continue on with as many cards as is necessary
using the same format.

I. Set 9 (temperature parameterization)

The parameterization of sets 9 to 11 (temperature, salin-
ity, and tidal height) is identical to the method of para-
meterization for solar radiation.

Card 1 FORMAT(4X,I2)

col 5-6   NUML = the number of line segments in the para-
meterization curve.

Card 2 FORMAT(11(1X,F6.2))

> CTEN = endpoints of each line segment.

> TT1 = y-axis intercept of each individual line
> segment.

> TT2 = slope of each line segment.

B-9

J. <u>Set 10 (salinity parameterization)</u>

  <u>Card 1</u> FORMAT(4X,I2)

  col 5-6 NUML = same as above.

  <u>Card 2</u> FORMAT(11(1X,F6.2))

      CSEN = same as above.

      SS1 = same as above.

      SS2 = same as above.

K. <u>Set 11 (tidal height parameterization)</u>

  <u>Card 1</u> FORMAT(4X,I2)

  col 5-6 NUML = same as above.

  <u>Card 2</u> FORMAT(11(1X,F6.2))

      CHEN = same as above.

      MH1 = same as above.

      MH2 = same as above.

8. The following example data are a card-image reproduction of the input cards needed to produce the results seen in Figures 50 to 55 of the main text.

```
    3    48   .20    1     1
   4.0       1200.   1.
    .9    .9    .9    .9
 S ALT
   5.0        600.   1.
    .9    .9    .9    .9
 D SPICATA
   5.0        600.   1.
    .9    .9    .9    .9
 S PATENS
  30.   20.    4.    6.
       6
   1.0  2.0   3.0   4.0   5.0   6.0
  .000  .000  .000  .000  .000  .000
      2     0    1     1     2
      2     1000.
      0
 PLANT BIOMASS
      2
   800.  1000.    0.     1.  .00125    0.
      2
   400.  1000.    0.0   1.66  .0025  -.0017
      2
   400.  1000.    0.0   1.66  .0025  -.0017
      3
  15.00  30.00  40.00   0.00   -.60   5.00    .01    .05   -.1
      3
  15.00  30.00  40.00   0.00   -.60   5.00    .01    .05   -.1
      3
  15.00  30.00  40.00   0.00   -.60   5.00    .01    .05   -.1
      1
  50.00   1.00   -.02
      3
   5.00  10.00  50.00   0.00   1.00   1.10    .20   0.00   -.01
      3
   5.00  10.00  50.00   0.00   1.00   1.10    .20   0.00   -.01
      5
   .025    .1    .6     .7     1.     0.    -.33    1.0    7.0    0.0    0.0
  13.33    0.   -10.    0.
      3
   .05     .1    1.     1.     2.     0.     0.   -20.     0.
      3
   .05     .1    1.     1.     2.     0.     0.   -20.     0.
```

Program Listing

9. The program listing is reproduced on pages B-12 through B-89.

GENERAL PROGRAM INFORMATION
=====

THE NUMBER OF SPECIES TO BE SIMULATED = 3
THE MAXIMUM NUMBER OF TIME INTERVALS = 48
THE INTEGRATION TIME INTERVAL = .2
THE PRODUCTIVITY ALGORITHM IS NUMBER 1

PLANT GROWTH INFORMATION
=====

SPECIE1 = S ALT , R = .0, PEAKB =1200.
SCALING FACTORS, LIGHT =.9 TEMP =.9 SAL =.9 TIDE = .9

SPECIE2 = D SPICATA, R = .3, PEAKB =600.
SCALING FACTORS, LIGHT =.9 SAL =.9 TIDE = .9

SPECIE3 = S PATENS , R = .3, PEAKB =600.
SCALING FACTORS, LIGHT =.9 TEMP =.9 SAL =.9 TIDE = .9

GENERAL STATISTICS

THE LATITUDE OF THE MARSH IS = 30.
THE MARSH CREEK SALINITY = 20.
THE MEAN TIDAL RANGE = 4.
THE SPRING TIDAL RANGE = 6.

SEDIMENT HEIGHT INFORMATION
=====

THE NUMBER OF DISCRETE HEIGHTS ARE6
THE ACTUAL HEIGHTS ARE = 1, 2, 3, 4, 5, 6.
DEPOSITION RATE EACH HEIGHT0. 0. 0. 0. 0. 0.

PLOT AND PRINT INFORMATION
————————————————

IFLAG = 2
NFLAG = 0
THE PLOT INTERVAL = 1
THE PRINT INTERVAL = 1
THE SPACING BETWEEN PLOTTED POINTS = 2
KFLAG = 2
THE OPERATOR SPECIFIED RANGE FOR THE X AXIS IS = 1000.
MFLAG = 0
THE LEGEND ON THE Y AXIS IS PLANT BIOMASS

COEFFICIENTS FOR THE PARAMETERIZATION CURVES
————————————————

LIGHT PARAMETERIZATION CURVES

THE NUMBER SEGMENTS FOR SPECIE 1 ARE 2
COEFFS SEGMENT 1 ARE 800. 0. .00125
COEFFS SEGMENT 2 ARE 1000. 1. 0.

THE NUMBER SEGMENTS FOR SPECIE 2 ARE 2
COEFFS SEGMENT 1 ARE 400. 0. .0025
COEFFS SEGMENT 2 ARE 1000. 1.66 -.0017

THE NUMBER SEGMENTS FOR SPECIE 3 ARE 2
COEFFS SEGMENT 1 ARE 400. 0. .0025
COEFFS SEGMENT 2 ARE 1000. 1.66 -.0017

TEMP PARAMETERIZATION CURVES

THE NUMBER SEGMENTS FOR SPECIE 1 ARE 3
COEFFS SEGMENT 1 ARE 15. 0. .01
COEFFS SEGMENT 2 ARE 30. -.6 .05
COEFFS SEGMENT 3 ARE 40. 5. -.1

THE NUMBER SEGMENTS FOR SPECIE 2 ARE 3
COEFFS SEGMENT 1 ARE 15. 0. .01
COEFFS SEGMENT 2 ARE 30. -.6 .05
COEFFS SEGMENT 3 ARE 40. 5. -.1

THE NUMBER SEGMENTS FOR SPECIE 3 ARE 3
COEFFS SEGMENT 1 ARE 15. 0. .01
COEFFS SEGMENT 2 ARE 30. -.6 .05
COEFFS SEGMENT 3 ARE 40. 5. -.1

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SALINITY PARAMETERIZATION CURVES

THE NUMBER SEGMENTS FOR SPECIE 1 ARE 1
COEFFS SEGMENT 1 ARE 50. 1. -.02

THE NUMBER SEGMENTS FOR SPECIE 2 ARE 3
COEFFS SEGMENT 1 ARE 5. 0. .2
COEFFS SEGMENT 2 ARE 10. 1. 0.
COEFFS SEGMENT 3 ARE 50. 1.1 -.01

THE NUMBER SEGMENTS FOR SPECIE 3 ARE 3
COEFFS SEGMENT 1 ARE 5. 0. .2
COEFFS SEGMENT 2 ARE 10. 1. 0.
COEFFS SEGMENT 3 ARE 50. 1.1 -.01

TIDE PARAMETERIZATION CURVES

THE NUMBER SEGMENTS FOR SPECIE 1 ARE 5
COEFFS SEGMENT 1 ARE .025 0. 0.
COEFFS SEGMENT 2 ARE .1 -.33 13.33
COEFFS SEGMENT 3 ARE .4 1. 0.
COEFFS SEGMENT 4 ARE .7 7. -10.
COEFFS SEGMENT 5 ARE 1. 0. 0.

THE NUMBER SEGMENTS FOR SPECIE 2 ARE 3
COEFFS SEGMENT 1 ARE .05 1. 0.
COEFFS SEGMENT 2 ARE .1 2. -20.
COEFFS SEGMENT 3 ARE 1. 0. 0.

THE NUMBER SEGMENTS FOR SPECIE 3 ARE 3
COEFFS SEGMENT 1 ARE .05 1. 0.
COEFFS SEGMENT 2 ARE .1 2. -20.
COEFFS SEGMENT 3 ARE 1. 0. 0.

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```
  1        PROGRAM SUCCESS(INPUT,OUTPUT,TAPE5=INPUT,TAPE6=OUTPUT)
           DIMENSION VAL(10,5,250),R(10),PEAKB(10),MT(20),MARE(5)
           DIMENSION ISPECIE(5),ICOEFF(5),S,250),PRINCO(10),LL(4,5),TT(4,5)
  5        DIMENSION DEP(20),RM(10),LSF(5),TSF(5),SSF(5),MSF(5),
          1CTEN(5,10),CSEN(5,10),CMEN(5,10),MURN(10),MURM(10),CLEN(5,10),
          2TT2(5,10),SS1(5,10),SS2(5,10),MM1(5,10),MM2(5,10)
           COMMON/TIDEF/VAL,KSPECIE=IMAX,ZLAT,ZMT,DT,PEAKB,R,DT,RANGE,ZSAL,
          1SPRING
 10        COMMON/PLOT/RFLAG,RSTART,IPLOTDT,NUR,NARE,INTE,GMAX,RFLAG,
          1NQ,NFLAG,MURNT,MT
          1CLEN=CTEN,CSEN=CMEN,LL1,LL2,TT1,TT2,SS1,SS2,MM1,MM2
           COMMON/ZIR/ICOEFF,ISPECIE,PRINCO
 15        REAL LSF,MSF,LL1,LL2,MM1,MM2,MT
     C  READ IN THE FOLLOWING INPUT DATA
     C  NUR - THE NUMBER OF PLANT SPECIES INCLUDED IN THE SIMULATION
 20  C  IMAX - THE MAXIMUM NUMBER OF TIME UNITS FOR THE SIMULATION (NORMYS)
     C  DT - THE TIME INTERVAL FOR THE INTEGRATION ROUTINE
     C  METHOD - PRODUCTIVITY ALGORITHM 1) LOGISTIC 2) MAX. PROD
     C  MCASE - NUMBER OF RUNS WITH DIFFERENT DATA SETS.
 25        WRITE(6,923)
 923       FORMAT(1H1)
           JCASE=0
           READ(5,100) NUR,IMAX,DT,METHOD,MCASE
           PRINT 0,,GENERAL PROGRAM INFORMATION ,
           PRINT 0,,,
 30        PRINT 200
           PRINT 0,,THE NUMBER OF SPECIES TO BE SIMULATED = 0,NUR
           PRINT 0,,THE MAXIMUM NUMBER OF TIME INTERVALS = 0,IMAX
           PRINT 0,,THE INTEGRATION TIME INTERVAL = 0,DT
           PRINT 0,,THE PRODUCTIVITY ALGORITHM IS NUMBER 0,METHOD
 35        PRINT 200
           PRINT 200
 200       FORMAT(1H0)
     C  THE FOLLOWING SPECIES-SPECIFIC INFORMATION WILL BE IMPUTED
 40  C  R(I) - INTRINSIC RATE OF INCREASE
     C  PEAKB(I) - PEAK STANDING CROP
     C  VAL(,I) - INITIAL BIOMASS
     C  SPECIE - SPECIE NAME, LESS THAN 10 CHARACTERS
 45        PRINT 0,,PLANT GROWTH INFORMATION,
           PRINT 0,,,,
        2  DO 3 I=1,NUR
           READ(5,101) R(I),PEAKB(I),VAL(1,1,1)
           READ(5,102) LSF(I),TSF(I),SSF(I),MSF(I)
 50        READ(5,903) ISPECIE(I)
           PRINT 200
           PRINT 0,,SPECIE=,I, 0,ISPECIE(I), R = 0,R(I), PEAKB =0,
          1PEAKB(I)
           PRINT 0,,SCALING FACTORS; LIGHT =0,LSF(I), TEMP =0,TSF(I), SAL =
 55       1=,SSF(I), TIDE = 0,MSF(I)
        3  CONTINUE
 903       FORMAT(A10)
```

```
      PRINT 200
      PRINT 200
C  READ IN MARSH CREEK DATA
C  ZSAL - AVERAGE CREEK SALINITY IN PARTS PER THOUSAND
C  RANGE - TIDAL RANGE IN FEET (SOURCE, TIDE TABLES)
C  SPRING - SPRING TIDAL RANGE IN FEET (SOURCE, TIDE TABLES)
C  ZLAT - THE LATITUDE OF THE SALT MARSH TO BE SIMULATED. THIS VALUE IS
C  EXPRESSED IN UNITS OF DEGREES

      READ(5,103) ZLAT,ZSAL,RANGE,SPRING
      PRINT *,GENERAL STATISTICS:
      PRINT *,
      PRINT 2C0
      PRINT *,THE LATITUDE OF THE MARSH IS = #,ZLAT
      PRINT *,THE MARSH CREEK SALINITY = #,ZSAL
      PRINT *,THE MEAN TIDAL RANGE = #,RANGE
      PRINT *,THE SPRING TIDAL RANGE = #,SPRING
      PRINT 200
      PRINT *,SEDIMENT HEIGHT INFORMATION:
      PRINT *,
      PRINT 200
C  READ IN SEDIMENT HEIGHT INFORMATION
C  NT(I) - THE HEIGHTS ALONG A TRANSECT FOR WHICH SIMULATION IS DESIRED.
C  THIS VALUE IS IN UNITS OF FEET ABOVE M.S.L.
C  DEP - DEPOSITION RATE FOR EACH HEIGHT IN THE SALT MARSH IN FEET/MONTH

      READ(5,104) NURMT
      READ(5,105) (HT(I),I=1,10)
      READ(5,106) (DEP(I),I=1,10)
      DO 3 I=1,NURMT
      DO 4 K=1,NUM
      VAL(I,K,1)=VAL(1,K,1)
    4 CONTINUE
    3 CONTINUE
      PRINT *,THE NUMBER OF DISCRETE HEIGHTS ARE,NURMT
      PRINT *,THE ACTUAL HEIGHTS ARE = #,(HT(I),I=1,NURMT)
      PRINT *,DEPOSITION RATE EACH HEIGHT=,(DEP(I),I=1,NURMT)
      PRINT 200
      PRINT 200
C  READ IN DATA TO SPECIFY IF PLOTTING OF OUTPUT, PRINTING OF OUTPUT,
C  OR BOTH ARE DESIRED.
C  IFLAG = 0, IF PLOTTING DESIRED
C  IFLAG = 1, IF PRINTING IS DESIRED
C  IFLAG = 2, IF BOTH ARE DESIRED
C  NFLAG=0, IF PLOTTING SPECIES THROUTH TIME AT A PARTICULAR STATION
C  NFLAG=1, IF PLOTTING A SPECIE THROUTH SPACE AND TIME
C  READ IN PRINT AND PLOT INFORMATION
C  IPLOTDT - PLOT INTERVAL (NUMBER OF UNIT TIME INTERVALS BETWEEN PLOTTED POINTS)
C  IPRINDT - PRINT INTERVAL (NUMBER OF UNIT TIME INTERVALS BETWEEN PRINTED POINTS
C  INTER = NUMBER OF SPACES ON GRAPHIC OUTPUT BETWEEN PLOTTED DATA

      WRITE(6,92)
      READ(5,107) IFLAG,NFLAG,IPLOTDT,IPRINDT,INTER
      PRINT *,PLOT AND PRINT INFORMATION:
```

```
115          PRINT 6,F------------------------------
             PRINT 200

      C READ IN THE FOLLOWING
      C RFLAG IS A DESIGNATION FOR HOW THE RANGE ON THE Y-AXIS IS COMPUTED
120   C RFLAG = 0 ALL VARIABLES ARE PLOTTED USING A COMBINED RANGE FOR THE Y-AXIS
      C RFLAG = 1 EACH VARIABLE IS PLOTTED USING A SEPERATE RANGE FOR THE Y-AXIS
      C COMPUTED WITHIN THE PROGRAM.
      C KFLAG = 2 ALL VARIABLES ARE PLOTTED USING A COMBINED RANGE FOR THE Y-AXIS
125   C WHICH IS SPECIFIED BY THE OPERATOR.
      C QMAX = SPECIFIED RANGE FOR THE Y-AXIS

             READ(5,1001) KFLAG,QMAX

      C READ IN THE FOLLOWING
130   C MFLAG SPECIFIES THE WIDTH OF THE OUTPUT GRAPH
      C MFLAG = 0, 100 CHARACTERS
      C MFLAG= 1, 80 CHARACTERS

             READ(5,1001) MFLAG
135
      C READ IN LEGEND INFORMATION
      C NAME IS THE LEGEND FOR THE Y-AXIS

             READ(5,996) (NAME(I),I=1,5)
140          PRINT 6,21FLAG = 6,21FLAG
             PRINT 6,9MFLAG = 6,MFLAG
             PRINT 6,9THE PLOT INTERVAL = 6,21PLOTOT
             PRINT 6,9THE PRINT INTERVAL = 6,21PRINOT
             PRINT 6,9THE SPACING BETWEEN PLOTTED POINTS = 6,INTER
145          PRINT 6,9KFLAG = 6,KFLAG
             PRINT 6,9THE OPERATOR SPECIFIED RANGE FOR THE X AXIS IS = 6,9QMAX
             PRINT 6,9MFLAG = 6,MFLAG
             PRINT 6,9THE LEGEND ON THE Y AXIS IS =,(NAME(I),I=1,5)
             PRINT 200
150    996   FORMAT(5A10)
             NAME=3HMON

      C READ IN COEFFICIENTS FOR PARAMETERIZATION CURVES
155   C LIGHT PARAMETERIZATION COEFFICIENTS

             DO 6 I=1,NUR
             READ(5,110) NUML(I)
             LARG1=NUML(I)
160          READ(5,111) (CLEN(I,J),J=1,LARG1),(CL11(I,K),K=1,LARG1),
            1(LL(Z(I,K),K=1,LARG1)
      6      CONTINUE

      C TEMPERATURE PARAMETERIZATION COEFFICIENTS
165
             DO 7 I=1,NUR
             READ(5,112) NUMT(I)
             LARG2=NUMT(I)
             READ(5,113) (CTEM(I,J),J=1,LARG2),(TT1(I,K),K=1,LARG2),
170         1(TT2(I,K),K=1,LARG2)
      7      CONTINUE
```

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```
      C SALINITY PARAMETERIZATION COEFFICIENTS
            DO 8 I=1,NUR
            READ(5,116) NUPS(I)
            LARG3=NUPS(I)
            READ(5,115) (CSEN(I,JJ),J=1,LARG3),(SS1E(I,K),K=1,LARG3),
           1(SS2E(I,K),K=1,LARG3)
          8 CONTINUE
      C TIDE PARAMETERIZATION COEFFICIENTS
            DO 9 I=1,NUP
            READ(5,116) NURM(I)
            LARG6=NURM(I)
            READ(5,117) (CHEN(I,JJ),J=1,LARG6),(HH1E(I,K),K=1,LARG6),
           1(HH2IE(I,K),K=1,LARG6)
          9 CONTINUE
        100 FORMAT(4X,I1,2X,I3,1X,F4.2,4X,I1,4X,I1)
        101 FORMAT(4(2X,F3.1))
        102 FORMAT(4(1X,F4.0))
        103 FORMAT(4X,I1)
        104 FORMAT(4X,I1)
        105 FORMAT(10(1X,F4.1))
        106 FORMAT(10(1X,F5.3))
        107 FORMAT(20(4X,I1),3(3X,I2))
        108 FORMAT(4X,I1,3X,I5,2X,I5,0)
        109 FORMAT(4X,I1)
        110 FORMAT(4X,I2)
        111 FORMAT(11(1X,F6.2))
        112 FORMAT(4X,I2)
        113 FORMAT(11(1X,F6.2))
        114 FORMAT(4X,I2)
        115 FORMAT(11(1X,F6.2))
        116 FORMAT(4X,I2)
        117 FORMAT(11(1X,F6.2))
            PRINT *,'COEFFICIENTS FOR THE PARAMETERIZATION CURVES'
            PRINT *,
            PRINT *,' LIGHT PARAMETERIZATION CURVES '
            PRINT 200
            DO 20 I=1,NUP
            IARG=NUPL(I)
            PRINT *,' THE NUMBER SEGMENTS FOR SPECIE ',I,' ARE ',NUPL(I)
            DO 21 K=1,IARG
            PRINT *,' COEFFS SEGMENT ',K,' ARE ',CLEN(I,K),LL1(I,K),LL2(I,K)
         21 CONTINUE
         20 CONTINUE
            PRINT *,' TEMP PARAMETERIZATION CURVES '
            PRINT 200
            DO 22 I=1,NUP
            PRINT *,' THE NUMBER SEGMENTS FOR SPECIE ',I,' ARE ',NURT(I)
            IARG=NURT(I)
            DO 23 K=1,IARG
            PRINT *,' COEFFS SEGMENT ',K,' ARE ',CTEN(I,K),TT1E(I,K),TT2E(I,K)
         23 CONTINUE
```

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```
      PRINT 200
   22 CONTINUE
      WRITE(6,921)
      PRINT 6,' SALINITY PARAMETERIZATION CURVES'
      PRINT 200
      DO 24 I=1,NUM
      PRINT 6,' THE NUMBER SEGMENTS FOR SPECIE 6,I, ARE 6,NUMS(I))
      IARG=NUMS(I)
      DO 25 K=1,IARG
      PRINT 6,' COEFFS SEGMENT 6,K, ARE 6,CSEN(I,K),SS1(I,K),SS2(I,K)
   25 CONTINUE
      PRINT 200
   24 CONTINUE
      PRINT 6,' TIDE PARAMETERIZATION CURVES'
      PRINT 200
      DO 26 I=1,NUM
      PRINT 6,' THE NUMBER SEGMENTS FOR SPECIE 6,I, ARE 6,NUMH(I)
      IARG=NUMH(I)
      DO 27 K=1,IARG
      PRINT 6,' COEFFS SEGMENT 6,K, ARE 6,CHEN(I,K),MM1(I,K),MM2(I,K)
   27 CONTINUE
      PRINT 200
   26 CONTINUE
      T=0.0
      J=0
      DO 18 I=1,NUM
      MM(I)=0
   18 CONTINUE
   17 CONTINUE
      J=J+5
      CALL SSPECIE(IRM,DEP)
      JM=MGO(J,24)
      IF(JM.EQ.0) T=0.0
      IF(JM.EQ.0) GO TO 30
      GO TO 31
   30 DO 32 I=1,NUP
      PM(I)=0
   32 CONTINUE
   31 JP=J/2
      IF(JP.LT.IMAT) GO TO 17
      IF(IFLAG.EQ.0) GO TO 11
      IF(IFLAG.EQ.1) GO TO 12
      CALL PLOT
      CALL PRINT (IPRINOT)
      GO TO 14
   11 CALL PLOT
      GO TO 14
   12 CALL PRINT(IPRINOT)
   14 CONTINUE
  999 IF(JCASE.LT.NCASE) GO TO 2
      STOP
      END
```

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```
1       SUBROUTINE SSPECIE(PM,DEP)
        DIMENSION VAL(10,5,250),R(10),PEAKB(10),PRIMCO(10),
       1ICCOEFF(10,5,250),
5      1TSF(5),SSF(5),MSF(5),PMT(10),SHADE(10),XID(10,10),PR(10),NT(20),
       2NARE(5),RN(10)=DEP(20)
        DIMENSION NURL(10),NURT(10),NUR(10),NURM(10),CLEM(5,10),
       ICTEM(5,10),CSEN(5,10),CMEN(5,10),LL1(5,10),LL2(5,10),TT1(5,10),
       2TIZ(5,10),SS1(5,10),SS2(5,10),MM1(5,10),MM2(5,10)
10      COMMON/TIDE/VAL,NKSPECIE,IPAR,ZLAT,ZHT,JJ,T,PEAKB,R,DT,RANGE,ZSAL,
       1SPRING
        COMMON/PLOT/RFLAG,RSTART,IPLOTDT,MUR,NARE,RARE,INTER,GMAX,NFLAG,
       1RG,NFLAG,NURMT,HT
        COMMON/PLANT/LSF,TSF,SSF,MSF,METHOD,NURL,NURT,NURS,NURM,
15     1CLEM,CTEM,CSEN,CMEM,LL1,LL2,TT1,TIZ,SS1,SS2,MM1,MM2
        COMMON/XXX/ICCOEFF,ISPECIE,PRIMCO
        REAL LSF,MSF,LL1,LL2,MM1,MM2,HT
C DETERMINATION OF ENVIRONMENTAL LEVELS FOR RADIATION, TEMPERATURE, SOIL
C SALINITY, AND TIDAL HEIGHT
20      ZZ=T
        MK=MCD(J,2)
        IF(MK.EQ.0) KP=J/2
        IF(J.EQ.1) KP=1
        DO 250 NN=1,NURMT
25      ZHT=PT(NN)-DEP(NN)
        DO 200 KO=1,NUR
        KSPECIE = KO
        IF(J.EQ.1) XID(NN,KSPECIE)=VAL(1,KSPECIE,1)
        ICCOEFF(NN,KSPECIE,RPJ=1HT
30      RR(KSPECIE)=R(KSPECIE)
        A=0.0
        ZLIGHT=LIT(ZLAT,T)
        ZTEMP=TEMP(ZLAT,T)
        IF((ZTEMP-15.).LT.(0.0)) ICCOEFF(NN,KSPECIE,RPJ=1HT
35      IF((NN,KSPECIE).EQ.0).AND.((ZTEMP-15.).LT.(0.0))) GO TO 30
        IF((ZTEMP-15.).LT.0.01.AND.(T.GT.(0.01))) GO TO 25
        MN(KSPECIE)=1
C DETERMINATION OF A SHADE COEFFICIENT FOR THE FINAL CALCULATION OF THE
C RADIATION LEVEL FOR A PARTICULAR SPECIES
        IF(RO.GT.1) GG TO 6
        DO 4 I=1,NUR
45      KSPEC=1
        PMT(I)=CCMTIRANGE(KSPEC,ZHT,PEAKB,J,XID,NN)
4       CONTINUE
6       SHADE(KSPECIE)=COSMADE(PMT,KSPECIE,NUR,ISPECIE)
        IF(SHADE(KSPECIE).LT.(0.0)) SHADE(KSPECIE)=0.0
50      ZLIGHT = SHADE(KSPECIE)*ZLIGHT
        CALL TIDE(ZHT,PERINUM,J,T,RANGE,SPRING)
        TTIDE=PERINUM
        SSAL=SAL(ZHT,T,SPRING,ZSAL)
C DETERMINATION OF LIMITING COEFFICIENTS AS A FUNCTION OF THE ABOVE
55 C ENVIRONMENTAL LEVELS
```

```
60          PRINCO(1)=COLIT(2)LIGHT+KSPECIE,NUM,CLEM,LL),LL2)+SF(KSPECIE)
            PRINCO(2)=COTEMP(TEMP,KSPECIE,NUM,CTEM,TT1,TT2)+TSF(KSPECIE)
            PRINCO(3)=COSSAL(SSAL,KSPECIE,NUM5,CSEN,SS1,SS2)+SSF(KSPECIE)
            PRINCO(4)=COTIDE(TTIDE,KSPECIE,NUM6,CMEN,MM1,MM2)+MSF(KSPECIE)
            IF(PRINCO(3).LE.(0.0)) PRINCO(3)=0.0
65          IF(PRINCO(4).LE.(0.0)) PRINCO(4)=0.0

C   DETERMINATION OF MINIMUM COEFFICIENT

            PRIM=PRINCO(1)
70          KKK=1
            DO 10 I=1,3
            IF(PRINCO(I+1).LT.PMIN) KKK=I+1
            IF(PRINCO(I+1).LT.PMIN) PRIM=PRINCO(I+1)
10          CONTINUE
75          IF(KKK.EQ.1) ICOEFF(NN,KSPECIE,KP)=1M1
            IF(KKK.EQ.2) ICOEFF(NN,KSPECIE,KP)=1M1
            IF(KKK.EQ.3) ICOEFF(NN,KSPECIE,KP)=1M5
            IF(KKK.EQ.4) ICOEFF(NN,KSPECIE,KP)=3MM
            PRING=PRIN+PEARB(KSPECIE)
80          IF(PRING.EQ.(0.0)) GO TO 20
            GO TO 30

C   THIS SECTION DETERMINES THE COEFFICIENTS FOR THE LOSS OF BIOMASS WHEN
C   THE PRODUCTIVITY CAN NOT SUSTAIN THE PRESENT STANDING CROP

85  20      IF(METHOD.EQ.1) A=((XXD(NN,KSPECIE)-PRIMB)/XXD(NN,KSPECIE))*.5
            IF(METHOD.EQ.2) A=.7
            RKSPECIE)=0.0
            PRIM=0.0
            GO TO 30
90  25      A=.99
            IF(METHOD.EQ.2) A=.9
            RKSPECIE)=0.0
            PRIM=0.0
95          ICOEFF(NN,KSPECIE,KP)=1MT

C   CALLING THE INTEGRATION ROUTINE

            30  CALL RUNGE(PRIMB,PM,A,XEQ,RETMOD,PRIM,NN,RKB,ZZ)
100 200     CONTINUE
            DO 300 I=1,NUM
            R(I)=RR(I)
300         CONTINUE
250         CONTINUE
            997 RETURN
105         END
```

B-21

```
        FUNCTION LIT(ZLAT,T)
        ZT=T
        F=(ZT+5)-1.5
        IF((ZLAT.LT.(26.2)) GO TO 5
        IF((ZLAT.LT.(28.7)).AND.(ZLAT.GE.(26.2))) GO TO 10
        IF((ZLAT.LT.(31.2)).AND.(ZLAT.GE.(28.7))) GO TO 15
        IF((ZLAT.LT.(33.7)).AND.(ZLAT.GE.(31.2))) GO TO 20
        IF((ZLAT.LT.(36.2)).AND.(ZLAT.GE.(33.7))) GO TO 25
        IF((ZLAT.LT.(38.7)).AND.(ZLAT.GE.(36.2))) GO TO 30
        IF((ZLAT.LT.(41.2)).AND.(ZLAT.GE.(38.7))) GO TO 35
        IF((ZLAT.LT.(43.7)).AND.(ZLAT.GE.(41.2))) GO TO 40
        LIT=173.598-29.5432*T+8.0955*(T**2)-.38080*(T**3)+
      15.15527E-03*(T**4)
        GO TO 50
      5 LIT=252.626-27.3595*T+.19515*(T**2)-6.71117E-02*(T**3)+
      11.3090E-03*(T**4)
        GO TO 50
     10 LIT=220.351-27.0140*T+.53222*(T**2)-8.43507E-02*(T**3)+
      11.4006E-03*(T**4)
        GO TO 50
     15 LIT=204.134-18.691*T+1.75523*(T**2)-.13225*(T**3)+
      11.9357E-03*(T**4)
        GO TO 50
     20 LIT=201.616+5.72725*T+3.31290*(T**2)-.19142*(T**3)+
      12.6845E-03*(T**4)
        GO TO 50
     25 LIT=165.139+11.3073*T+3.89760*(T**2)-.23327*(T**3)+
      13.2622E-03*(T**4)
        GO TO 50
     30 LIT=151.49-8.1054*T+5.65282*(T**2)-.29468*(T**3)+
      14.0064E-03*(T**4)
        GO TO 50
     35 LIT=173.450-24.319*T+7.4158*(T**2)-.35977*(T**3)+
      14.7708E-03*(T**4)
        GO TO 50
     40 LIT=169.154-22.2119*T+6.6080*(T**2)-.31744*(T**3)+
      14.1660E-03*(T**4)
     50 CONTINUE
        T=ZT
        RETURN
        END
```

```
        FUNCTION TEMP(ZLAT,T)
        IF((ZLAT.LT.(26.21)) GO TO 5
        IF((ZLAT.LT.(28.71).AND.(ZLAT.GE.(26.21))) GO TO 10
        IF((ZLAT.LT.(31.21).AND.(ZLAT.GE.(28.71))) GO TO 15
        IF((ZLAT.LT.(33.71).AND.(ZLAT.GE.(31.21))) GO TO 20
        IF((ZLAT.LT.(36.21).AND.(ZLAT.GE.(33.71))) GO TO 25
        IF((ZLAT.LT.(38.71).AND.(ZLAT.GE.(36.21))) GO TO 30
        IF((ZLAT.LT.(41.21).AND.(ZLAT.GE.(38.71))) GO TO 35
        IF((ZLAT.GE.(41.21).AND.(ZLAT.GE.(41.21))) GO TO 40
        TEMP=-7.53394-2.20082*(T)+1.90010*(T**2)-7.78654E-02*(T**3)-
       11.76025E-02*(T**4)+1.01810E-03*(T**5)
        GO TO 50
      5 TEMP=21.1939-1.47460*(T)+.80498*(T**2)-9.79302E-02*(T**3)+
       12.79377E-03*(T**4)
        GO TO 50
     10 TEMP=17.6671-1.58900*(T)+1.25803*(T**2)-.15603*(T**3)+
       15.04764E-03*(T**4)
        GO TO 50
     15 TEMP=13.9412-.64429*(T)+.91001*(T**2)-.06507*(T**3)-
       18.53603E-03*(T**4)+5.27905E-04*(T**5)
        GO TO 50
     20 TEMP=10.872-2.2778*(T)+1.9672*(T**2)-.24430*(T**3)
       18.13280E-03*(T**4)
        GO TO 50
     25 TEMP=-7.26697-1.06746*(T)+1.10513*(T**2)-1.07108E-02*(T**3)
       1-1.49458E-02*(T**4)+7.73001E-04*(T**5)
        GO TO 50
     30 TEMP=4.22511-4.33856*(T)+.00086*(T**2)-.37050*(T**3)+
       11.01251*(T**4)
        GO TO 50
     35 TEMP=.41176-3.00803*(T)+2.2791*(T**2)-.12500*(T**3)-
       11.61790E-02*(T**4)+1.07460E-03*(T**5)
        GO TO 50
     40 TEMP=-3.54638-2.07603*(T)+2.08069*(T**2)-.10437*(T**3)-
       11.68912E-02*(T**4)+1.06638E-03*(T**5)
     50 CONTINUE
        RETURN
        END
```

```
      FUNCTION SAL(ZMT,TP,SPRING,ZSAL)
      ZM=ZMT/SPRING
      IF(ZM.LT.(.75)) SAL=ZSAL
      IF((ZM.GE.(.75)).AND.(ZM.LT.(1.1))) SAL=(-1.1127+2.8579*ZM)*ZSAL
      IF(ZM.GT.(1.1)) SAL=ZSAL*(6.75-2.5*ZM)
      RETURN
      END
```

```
FUNCTION CONT    73/172  OPT=1           FTN 4.6+433      03/31/77  22.51.39    PAGE   1


 1         FUNCTION CONT(RANGE,KSPEC,ZHT,PEAKB,J,XXD,NN)
           DIMENSION PEAKB(10),XXD(10,10)
           GO TO (10,20,30,40,50) KSPEC
 5      10 IF(XXD(NN,KSPEC).LE.(0.0)) CONT=0.0
           IF(XXD(NN,KSPEC).LE.(0.0)) GO TO 60
           CONT=RANGE*XXD(NN,KSPEC)/PEAKB(KSPEC)
           GO TO 60
10      20 CONT=XXD(NN,KSPEC)*0.006
           GO TO 60
        30 CONTINUE
           CONT=XXD(NN,KSPEC)*0.006
           GO TO 60
15      40 CONTINUE
           CONT=1.0
           GO TO 60
        50 CONTINUE
           CONT=1.0
2C      60 CONTINUE
           RETURN
           END
```

B-25

```
1        FUNCTION COSMADE(PNT,ISPECIE,NUM,ISPECIE)
         DIMENSION PNT(10),ISPECIE(5)
         PMAXMT=0.0
5        DO 10 I=1,NUR
         AMT=PNT(I)-PNT(KSPECIE)
         IF(AMT.GT.PMAXMT) PMAXMT = AMT
         IF(AMT.GT.PMAXMT) K=I
10       CONTINUE
         IF(PMAXMT.LE.(0.0)) COSMADE=1.0
         IF(PMAXMT.LE.(0.0)) GO TO 20
         IF(PMAXMT.GT.(0.0)) Z=PMAXMT
         IF((ISPECIE(K).EQ.8HS PATENS).OR.(ISPECIE(K).EQ.9HD SPICATA))
         1 GO TO 25
15       IF(Z.LE.(.45)) COSMADE=1.0-1.53535E+02
         IF(Z.GT.(.45)) COSMADE=.35241-.11764702
         IF(Z.GT.(3.0)) COSMADE=0.0
         GO TO 20
25       IF(Z.LE.(.11)) COSMADE=1.0-6.16035E02
20       IF((Z.GT.(.11)).AND.(Z.LE.(.6))) COSMADE=.37037-.61728E02
         IF(Z.GT.(.6)) COSMADE=0.0
20       RETURN
         END
```

```
 1        FUNCTION COLIT(ZLIGHT,NSPECIE,NUML,CLEN,LL1,LL2)
          DIMENSION NUML(10),CLEN(5,10),LL1(5,10),LL2(5,10)
          REAL LL1,LL2
          N=NSPECIE
          Z=ZLIGHT
          IARG=NUML(N)
 5        DO 10 I=1,IARG
          IF((Z.LE.CLEN(N,I)).AND.(Z.GE.(0.0))) COLIT=LL1(N,I)+Z*LL2(N,I)
          IF((Z.EQ.I) GO TO 10
          IF((Z.LE.CLEN(N,I)).AND.(Z.GT.CLEN(N,I-1))) COLIT=LL1(N,I)+Z0
 10       CONTINUE
          RETURN
          END
```

B-27

```
        FUNCTION COTEMP(ZTEMP,NSPECIE,NURT,CTEM,TT1,TT2)
        DIMENSION NURT(10),CTEM(5,10),TT1(5,10),TT2(5,10)
        N=NSPECIE
        Z=ZTEMP
        IARG=NURT(N)+1
        DO 10 I=1,IARG
        IF((Z.LE.CTEM(N,1)).AND.(Z.GE.(0.0))) COTEMP=TT1(N,1)+Z*TT2(N,1)
        IF((Z.GT.0.1) GO TO 10
        IF((Z.LE.CTEM(N,1)).AND.(Z.GT.CTEM(N,1-1))) COTEMP=TT1(N,1)+Z*
     1  TT2(N,1)
   10   CONTINUE
        RETURN
        END
```

```
FUNCTION COSSAL(SSAL,MSPECIE,NUM5,CSEN,SS1,SS2)
DIMENSION NUM5(10),CSEN(5,10),SS1(5,10),SS2(5,10)
Z=SSAL
N=MSPECIE
IARG=NUM5(N)
DO 10 I=1,IARG
IF((Z.LE.CSEN(N,1)).AND.(Z.GE.(0.0)) COSSAL=SS1(N,1)+Z*SS2(N,1)
IF(I.EQ.1) GO TO 10
IF((Z.LE.CSEN(N,I)).AND.(Z.GT.CSEN(N,I-1))) COSSAL=SS1(N,I)+Z*
1SS2(N,1)
10 CONTINUE
RETURN
END
```

```
 1       FUNCTION COTIDE(TTIDE,KSPECIE,NUMM,CHEM,MM1,MM2)
         DIMENSION NUMM(10),CHEM(5,10),MM1(5,10),MM2(5,10)
         REAL MM1,MM2
         N=KSPECIE
 5       Z=TTIDE
         IARG=NUMM(N)
         DO 10 I=1,IARG
         IF((Z.LE.CHEM(N,1)).AND.(Z.GE.(0.0))) COTIDE=MM1(N,1)+Z*MM2(N,1)
         IF(Z.EQ.J) GO TO 10
         IF((Z.LE.CHEM(N,1)).AND.(Z.GT.CHEM(N,I-1))) COTIDE=MM1(N,I)+Z*
        1MM2(N,1)
10       CONTINUE
         RETURN
         END
```

```
       1          SUBROUTINE TIDE(ZMT,PERINUM,J,T,RANGE,SPRING)
                  ZEM=ZMT/RANGE
                  PI=3.1417
       C   TIDE INUNDATION PER MONTH IS BASED ON THE YEARLY TIDAL INUNDATION CURV
       5   C   TAKING INTO ACCOUT A TWINCE YEARLY SINUSOIDAL CURVE CORRECTION
                  IF(ZZM.LT.(1.0)) PER:NUM=1.0-.95*ZZM
                  IF(PERINUM.GT.1.0) PERINUM=1.0
                  IF(ZZM.GE.(1.0)) PERINUM=.201-.151*ZZM
                  IF(ZZM.GT.(1.33)) PERINUM=0.0
      10          IF(PERINUM.LE.(0.0)) PERINUM=0.0
                  RETURN
                  END
```

B-31

```
         SUBROUTINE RUNGE(PRIM,MM,A,RHO,METHOD,PRIM,MM,KK2,ZZ)
         DIMENSION XHD(10,10),XD(12,5),VAL(10,5,230),X(12,5),R(10),
        2PEAKB(10),ZZ,JJ(10,10)
         DIMENSION MARE(5),MM(10),PT(20)
         COMMON/TIDE/VAL,KSPECIE,INA,ZLAT,ZMT,J,T,PEAKB,R,DT,RANGE,ZSAL,
   5SPRING
         COMMON/PLOT/RFLAG,ISTART,IPLOT,NUM,MARE,MARE,INTB,QMAX,RFLAG,
         1PO,NFLAG,NLPNT,MT
         IF(I.EQ.1).AND.(MM.EQ.1)) MO=1
         IF(MM(KSPECIE).EQ.0) GO TO 800
  10     IF(METHOD.EQ.2) GO TO 700
         JM=0
         T=ZZ
         JNUM=1.0/DT+1
         IF(J.EQ.-3) JJ(MM,KSPECIE)=0
  15  10 CONTINUE
         IF(JJ(MM,KSPECIE).EQ.1) GO TO 800
  20  20 DO 300 K=1,4
         IF(K.EQ.1) GO TO 300
         IF(K.EQ.4) GO TO 150
 100     X(1,K)=XD(MM,KSPECIE)+DT/2.0*(XD(1,K-1))
         GO TO 400
 130     X(1,K)=XD(MM,KSPECIE)+DT*(XD(1,K-1))
         GO TO 400
 300     X(1,K)=XD(MM,KSPECIE)
 25  400 CONTINUE
         IF(PRIM.EQ.10.01) XD(1,K)=-A*X(1,K)
         IF(PRIM.EQ.10.01) GO TO 500
         IF(METHOD.EQ.1)  XD(1,K)=RKSPECIE)*X(1,K)*((PRIM-R(1,K))/
 30  1PRIMB)-A*X(1,K)
 500     CONTINUE
         XD(MM,KSPECIE)=XD(MM,KSPECIE)+DT/6.0*(XD(1,1)+2.0*XD(1,2)+2.0*
         3XD(1,3)+XD(1,4))
         IF(XD(MM,KSPECIE).LE.VAL(1,KSPECIE,1)) XD(MM,KSPECIE)=
 35  1VAL(1,KSPECIE,1)
         IF(XD(MM,KSPECIE).LE.10..AND.T.GT.7.) XD(MM,KSPECIE)=
         1VAL(1,KSPECIE,1)
         IF(XD(MM,KSPECIE).EQ.VAL(1,KSPECIE,1)) GO TO 800
 40  700 CONTINUE
         JM=JM+1
         IF(JM.LT.JNUM) GO TO 10
         IF(METHOD.EQ.2.AND.A.EQ.0.0) XD(MM,KSPECIE)=PRIM*PEAKB(KSPECIE)
 45      IF(METHOD.EQ.2.AND.A.NE.0.0) XD(MM,KSPECIE)=XD(MM,KSPECIE)=-A*
         1XD(MM,KSPECIE)
         IF(METHOD.EQ.2.AND.XD(MM,KSPECIE).LT.VAL(1,KSPECIE,1))
         1XD(MM,KSPECIE)=VAL(1,KSPECIE,1)
 50  800 JB=IPLOT/DT+2
         MA=MOD(J,JB)
         IF(KSPECIE.GT.1) GO TO 801
         IF((MA.EQ.0).AND.(MM.EQ.1)) MO=MO+1
         IF(J.EQ.2.AND.MM.EQ.1) MO=1
 55  801 IF(MA.EQ.0) VAL(MM,KSPECIE,MO)=XD(MM,KSPECIE)
         RETURN
         END
```

```
SUBROUTINE PLOT
1          DIMENSION CLEAN(10),LINE(10),TVAL(5),P(20),LABEL(20)
           DIMENSION VAL(10,5,25),NAME(5),VMAX(10),ISPEC(15)
           DIMENSION PRINCQ(10),ICOEFF(10,3,25),PEAKB(10),R(10)
5          DIMENSION LSF(5),TSF(5),SSF(5),MSF(5),MT(20)
           DIMENSION NURL(10),NUPT(10),NURS(10),NUPM(10),CLEN(5,10),
          1CTEM(5,10),CSEN(5,10),CMEN(5,10),LL1(5,10),LL2(5,10),TT1(5,10),
          2TT2(5,10),SS1(5,10),SS2(5,10),MM1(5,10),MM2(5,10),
          CCOMMON/TIDE/VAL,RSPECIE,IMAX,ZLAT,ZINT,J,T,PEAKB,R,DT,RANGE,ZSAL,
10   1SPRING
           COMMON/PLOT/MFLAG,ISTART,IPLCIDT,NUM,NAME,NAME,INTER,GMAX,MFLAG,
          1NQ=MFLAG=NUMT=NT
           COMMON/PLANT/LSF,TSF,SSF,MSF,METHOD,NURT,NURS,NUM,
          1CLEN,CTEM,CSEN,CMEN,LL1,LL2,TT1,TT2,SS1,SS2,MM1,MM2
           COMMON/XXX/ICCOEF,ISPECIE,PRINCQ
15         REAL LSF,MSF,LL1,LL2,MM1,MM2,MT
           INTEGER CLEAN,LINE,P,DOT,BLANK,STAR
           DATA DOT,BLANK,STAR/1H.,1H ,1H*/
100        FORMAT(////,E1H1)
           FORMAT(13X,3(1OX,F10.1),3H.,OPRINCQ)
20   101   FORMAT(/35X,5A10)
102        FORMAT(13X,101A1)
103        FORMAT(13X,101A1)
104        FORMAT(2H,F5.0,2H,A3,1H,101A1)
105        FORMAT(35X,5(3X,F7.1),3H,OPRINCQ)
25   106   FORMAT(/15X,5A10)
114        FORMAT(13X,51A1)
107        FORMAT(2X,F5.0,2H,A3,1H,51A1,6X,A1,9X)
116        FORMAT(2X,F5.0,2H,A3,1H,51A1,6X,5A1)
117        FORMAT(2X,F5.0,2H,A3,1H,101A1,9X,10A1)
30   119   FORMAT(2X,F5.0,2H,A3,1H,101A1,6X,5A1)
           KNUM=0
5          CONTINUE
           KNUM=KNUM+1
           ZNT=NT(KNUM)
35         I=0,0
           KJ=IPLOTDT
           K=0
           NMAX=0
           JPT=NMAX-1
40         P(1)=1H1
           P(2)=1H2
           P(3)=1H3
           P(4)=1H4
           P(5)=1H6
45         P(6)=1H6
           P(7)=2H7
           P(8)=1H8
           P(9)=1H9
           IF(MFLAG.EQ.0) GO TO 6
50         DO 10 I=1,NURMT
           VMAX(I)=VAL(I,KNUM,1)
           DO 15 I7=3,JPT
           IF((VAL(I,KNUM,IV+1)).GT.(VMAX(I))) VMAX(I)=VAL(I,KNUM,IV+1)
15         CONTINUE
55   10    CONTINUE
           GO TO 61
6          DO 60 I=1,NUR
```

```
              VMAX(I)=VAL(KNUM,I=1)
              DO 50 IY=1,JPT
              IF((VAL(KNUM,I,IY+1)).GT.(VMAX(I))) VMAX(I)=VAL(KNUM,I,IY+1)
        50    CONTINUE
        60    CONTINUE
        61    IF(KFLAG.EQ.1) GO TO 65
              JK=NUM-1
              IF(JK.LT.1) GO TO 65
              IF(KFLAG.EQ.0) GO TO 66
              JG=KUFMT-1
              DO 80 I=1,JG
              IF(VMAX(I)().GT.VMAX(I)) VPAT(I)=VMAX(I,1)
        80    CONTINUE
              GO TO 65
        66    DO 70 I=1,JK
              IF(VMAX(I)(1).GT.VMAX(I)) VMAX(I)=VMAX(I)(1)
        70    CONTINUE
        65    CONTINUE
              IF(KFLAG.EQ.2) VMAX(I)=GRAX
              PRINT 100
        121   FORMAT(1H0)
              PRINT 121
              IF(KFLAG.EQ.0) PRINT *,*             LATITUDE = 0,ZLAT,0   CREEK SAL = 0,ZSAL
        ING TIDE = 0,SPRING,0                    MEAN TIDE = 0,RANGE,0   SPRI
              IF(KFLAG.EG.1) PRINT *,*            MARSH HEIGHT = 0,JHT
        ING TIDE = 0,SPRING                      MEAN TIDE = 0,RANGE,0   SPRI
              PRINT 110
              IF(KFLAG.EQ.1) PRINT *,*                        PLANT,RNUM,= 0,
        115SPECIE(KKNUM),0   R = 0,BERMUD,0, PEAK STANDING CROP = 0,
        ZPEAKBKNUM)
              IF(KFLAG.EQ.1) GO TO 88
              DO 67 RESPEC=1,AUM
              PRINT *,*                          PLANT,KKSPEC,0 = 0,ISPECIE(KKSPEC),0  R
        1 = 0,BERK(KKSPEC),0  PEAK STANDING CROP = 0,PEAK(KKSPEC)
        87    CONTINUE
        88    PRINT 110
              PRINT 110
              IF(KFLAG.EQ.1) GO TO 777
              PRINT 102,(MAME(I),I=1,5)
              GO TO 782
        777   PRINT 106,(MAME(I),I=1,5)
        782   DO 100 I=1,NUM
        201   DO 100 K=1,5
        106   TVAL(K)=(VMAX(I)/5.00)*FLOAT(K)
              IF(KFLAG.EQ.1) GO TO 778
              PRINT 101,(TVAL(K),K=1,5)
              GO TO 783
        778   PRINT 105,(TVAL(K),K=1,5)
        783   CONTINUE
        100   CONTINUE
        120   CONTINUE
              KQ=101
              IF(KFLAG.EQ.1) KQ=51
              DO 110 K=2,KQ
```

```
115        LINE(K)=DOT
           M=MOD(K-1,20)
           IF(MFLAG.EQ.1) M=MOD(K-1,10)
           IF(M.EQ.0) LINE(K)=STAR
120        CONTINUE
           LINE(1)=DOT
           IF(MFLAG.EQ.1) GO TO 781
           PRINT 103,LINE
           GO TO 784
781        PRINT 114,(LINE(II),II=1,51)
125 784    CONTINUE
111        LINE(K)=BLANK
           NNUM=NUM
           IF(MFLAG.EQ.1) NNUM=MNUMNT
130        DO 116 K=1,MMAX
           DO 112 I=1,MNUM
           IF(MFLAG.EQ.1) GO TO 210
           IF(MFLAG.EQ.1).AND.(VAL(I,KNUM,K).GT.VMAX(I))) VAL(I,KNUM,K)=
          1VMAX(I)
135        IF(MFLAG.EQ.0).AND.(VAL(KNUM,I,K).GT.VMAX(I))) VAL(KNUM,I,K)=
          1VMAX(I)
           IF(MFLAG.EQ.0) M=100.*((VAL(KNUM,I,K)-VMAX(I))/VMAX(I))+1.0)+1.5
           IF(MFLAG.EQ.1) M=100.*((VAL(I,KNUM,K)-VMAX(I))/VMAX(I))+1.0)+1.5
           IF(MFLAG.EQ.1) M=50.*((VAL(KNUM,I,K)-VMAX(I))/VMAX(I))+1.5
140        IF((MFLAG.EQ.1).AND.(MFLAG.EQ.1)) M=50.*((VAL(I,KNUM,K)-VMAX(I))
          1/VMAX(I))+1.0)+1.5
           GO TO 220
210        IF((MFLAG.EQ.0).AND.(VAL(KNUM,I,K).GT.VMAX(I))) VAL(KNUM,I,K)=
          1VMAX(I)
145        IF((MFLAG.EQ.1).AND.(VAL(I,KNUM,K).GT.VMAX(I))) VAL(I,KNUM,K)=
          1VMAX(I)
           IF(MFLAG.EQ.0) M=100.*((VAL(KNUM,I,K)-VMAX(I))/VMAX(I))+1.0)+1.5
           IF(MFLAG.EQ.1) M=100.*((VAL(I,KNUM,K)-VMAX(I))/VMAX(I))+1.0)+1.5
           IF(MFLAG.EQ.1) M=50.*((VAL(KNUM,I,K)-VMAX(I))/VMAX(I))+1.5
150        IF((MFLAG.EQ.1).AND.(MFLAG.EQ.1)) M=50.*((VAL(I,KNUM,K)-VMAX(I)))
          1VMAX(I))+1.0)+1.5
220        CONTINUE
           IF(M.LE.0) M=1
           LINE(M)=P(I)
112        CONTINUE
155        JZ=K+IPLOTDT
           JFCK.EQ.1) JZZ=1
           KK=IPLOTDT
           IF(MFLAG.EQ.1) GO TO 779
           LINE(1)=STAR
160        IF(MFLAG.EQ.0) PRINT 119,Z,RARE,LINE,((COEFF(KNUM,KSP,JZZ),
          1KSP=1,NUM)
           IF(MFLAG.EQ.1) PRINT 117,Z,RARE,LINE,((COEFF(K,KNUM,JZZ),
          1KE=1,MNUMNT)
           GO TO 785
165 779    IF(MFLAG.EQ.0) PRINT 118,Z,RARE,(LINE(II),II=1,51),
          1((COEFF(KNUM,KSP,JZZ),KSP=1,NUM)
           IF(MFLAG.EQ.1) PRINT 118,Z,RARE,(LINE(II),II=1,51),
170        1((COEFF(K,KNUM,JZZ),KE=1,MNUMNT)
785        CONTINUE
```

```
        DO 115 I=1,NNUM
        ICLEAN=CLEAN(I)
        LINE(ICLEAN)=BLANK
115     CONTINUE
175     IF(K.EQ.MAX) GO TO 116
        IF(INTER.EQ.0) GO TO 116
        DO 300 I=1,INTER
        LINE(I)=DOT
180     IF(INFLAG.EQ.1) GO TO 780
        PRINT 103,LINE
        GO TO 786
780     PRINT 114,(LINE(II),II=1,91)
786     CONTINUE
185     300 CONTINUE
116     CONTINUE
        IF((INFLAG.EQ.1).AND.(KNUM.LT.NUM)) GO TO 5
        IF((INFLAG.EQ.0).AND.(KNUM.LT.NUM7)) GO TO 5
190     RETURN
        END
```

```
 1        SUBROUTINE PRINT(IPRINDT)
          DIMENSION VAL(10,5,250),NAME(5)
          DIMENSION PEAKB(10),R(10),MT(20)
          COMMON/TIDEE/VALKSPECIE,IMAX,ZLAT,ZHT,J,T,PEAKB,R,DT,RANGE,ZSAL,
 5       1SPRING
          COMMON/PLOT/KFLAG,XSTART,IPLOTDT,NUM,NAME,INTER,QMAX,MFLAG,
         1MQ,NFLAG,NUMMT,MT
          WRITE(6,907)
907       FORMAT(1H1)
10        WRITE(6,100)
100       FORMAT(20,*BIOMASS AS A FUNCTION OF TIME*)
          WRITE(6,210)
210       FORMAT(1HO)
          JANE=3HMCM
15        KNUR=NUR
          MMAX=MQ
          MP=MMAX/IPRINDT
          MK=0
 5        CONTINUE
20        NK=NK+1
          WRITE(6,211) MK
211       FORMAT(30Z,*MARSH WEIGHT = *,I1)
          WRITE(6,210)
          GO TO (101,102,103,104),KNUR
25    101 WRITE(6,200) JANE
200       FORMAT(10X,*TIME*,A5,7X,*SPECIE 10)
          GO TO 105
102       WRITE(6,201) JANE
201       FORMAT(10X,*TIME*,1X,A5,7X,*SPECIE 20)
30        GO TO 105
103       WRITE(6,202) JANE
202       FORMAT(10X,*TIME*,1X,A5,7X,*SPECIE 20,7X,*SPECIE 30)
          GO TO 105
104       WRITE(6,203) JANE
35    203 FORMAT(10X,*TIME*,1X,A5,7X,*SPECIE 20,7X,*SPECIE 30,
         17X,*SPECIE 40)
105       CONTINUE
          WRITE(6,114)
114       FORMAT(1HO)
40        DO 50 I=1,MP
          L=I*IPRINDT
          GO TO (110,111,112,113),KNUR
110       WRITE(6,204) L,(VAL(MK,K,1),K=1,KNUR)
204       FORMAT(11X,I3,10X,F10.3)
45        GO TO 50
111       WRITE(6,205) L,(VAL(MK,K,I),K=1,KNUR)
205       FORMAT(11X,I3,5X,2(5X,F10.3))
          GO TO 50
112       WRITE(6,206) L,(VAL(MK,K,1),K=1,KNUR)
50    206 FORMAT(11X,I3,5X,3(5X,F10.3))
          GO TO 50
113       WRITE(6,207) L,(VAL(MK,K,1),K=1,KNUR)
207       FORMAT(11X,I3,5X,4(F10.3))
 50       CONTINUE
55        WRITE(6,210)
          IF(NK.LT.NUMMT) GO TO 5
          RETURN
```

SUBROUTINE PRINT   73/172   OPT-1   FTN 4.6+433   03/31/77   22:51:39   PAGE   2

END

MARSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
AV1	01	73	186	S.ALT	LIVE	372.3	102.3	440.0	80.0		
AV1	01	73	186	SALIC	LIVE	7.0		150.0	30.0		
AV1	07	73	186	T.DEAD	DEAD	62.9	22.3				
AV1	02	73	186	S.ALT	LIVE	254.7	28.0	970.0	110.0		
AV1	03	73	186	SALIC	LIVE	37.2	12.8	30.0	490.0		
AV1	03	73	186	S.ALT	LIVE	100.9	29.7				
AV1	06	73	186	S.ALT	LIVE	182.2	196.6	250.0	150.0		
AV1	06	73	186	T.DEAD	DEAD	11.7		530.0	110.0		
AV1	06	73	186	S.ALT	LIVE	156.1	13.7				
AV1	06	73	186	T.DEAD	DEAD	238.1	27.7				
AV1	05	73	186	UNK	LIVE	95.4					
AV1	05	73	186	S.ALT	LIVE	.8	70.0	370.0	550.0		
AV1	05	73	186	S.ALT	DEAD	165.0	51.8				
AV1	05	73	186	PHRAG	LIVE	326.2					
AV1	05	73	186	SALIC	LIVE	112.0	120.0				
AV1	05	73	186	T.DEAD	DEAD	7.4	40.0				
AV1	05	73	186			643.8					
AV1	05	73	186	UNK	LIVE	3.8	80.0				

MARSH SAMPLE DEPTH YEAR DAY SPECIE PH EH ORGANIC MATTER STD. ERR. MEAN

MARSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
BAY	01	74	170	S.ALT	LIVE	240.0		32.0		72.	
BAY	01	74	170	S.ALT	DEAD	51.0					
BAY	01	74	170	S.ALT	LITTER	64.0					
BAY	01	74	238	S.ALT	DEAD	38.0					
BAY	02	74	170	S.ALT	DEAD	317.0		184.0		012.	
BAY	02	74	170	S.ALT	LIVE	102.0					
BAY	02	74	238	S.ALT	LITTER	84.0		300.0		129.	
BAY	02	74	238	S.ALT	LIVE	315.0		320.0		792.	
BAY	03	74	170	S.ALT	DEAD	77.0					
BAY	03	74	170	S.ALT	LIVE	365.0		808.0		42.	
BAY	03	74	238	S.ALT	LITTER	216.0		202.0		010.	
BAY	04	74	170	S.ALT	DEAD	213.0					
BAY	04	74	170	S.ALT	LIVE	36.0		690.0		750.	
BAY	04	74	170	D.SPI	DEAD	1.0					
BAY	04	74	170	D.SPI	LITTER	74.0					
BAY	04	74	170	SALIC	LIVE	29.0					
BAY	05	74	170	D.SPI	DEAD	130.0		320.0		135.	
BAY	05	74	170	D.SPI	LITTER	137.0					
BAY	05	74	170	SALIC	LITTER	35.0					
BAY	05	74	170	D.SPI	DEAD	11.0					
BAY	05	75	170	D.SPI	LIVE	568.0				2.	
BAY	05	75	238	D.SPI	LITTER	44.0					
BAY	10	75	238	S.ALT	LITTER	41.0	80.1	398.7	36.1		
BAY	11	75	230	S.ALT	DEAD	901.2	2.6				
BAY	11	75	230	S.ALT	DEAD	154.5	75.1	212.0	17.4		
BAY	01	74	238	S.ALT	DEAD	831.7	85.8	100.0		91.	
BAY				S.ALT	LIVE	254.3					
BAY						266.0					

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	PH	EH	ORGANIC MATTER	STD. ERR. MEAN
	02	0	75	88	S.ALT			14.0	
	02	10	75	88	S.ALT				
	02	20	75	88	S.ALT				
	02	30	75	88	S.ALT	6.3	-420		
	03	0	75	88	S.ALT	6.5	-450		
	03	100	75	88	S.ALT				
	10	0	75	88	S.ALT				
	10	200	75	88	S.ALT	6.6	-280		
	11	0	75	88	S.ALT	7.0	-325		
	11	100	75	88	S.ALT	7.0	-360	13.0	
	11	30	75	88	S.ALT				

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	NH4	STD. ERR.	PO4	STD. ERR.	IRON	STD. ERR.	NH	STD. ERR.
BAV	02	0	75	00	S.ALT	20.37		106.0	10.8	1002.3	58.1		
BAV	02	10	75	00	S.ALT	26.33		81.8	21.9	356.2	5.3		
BAV	02	20	75	00	S.ALT	11.28		70.5		127.9	10.6		
BAV	03	0	75	00	S.ALT	9.35		131.9	14.2	266.8	.1		
BAV	03	10	75	00	S.ALT	25.03		110.4	13.2	377.2			
BAV	03	20	75	00	S.ALT	7.63		160.0	64.8	429.3	100.1		
BAV	03	30	75	00	S.ALT	5.23		64.0	6.2	112.7	5.8		
BAV	05	0	75	00	14-OS			90.5	28.8	181.0	86.1		
BAV	05	0	75	00	D.SPI			114.6	19.3				

MARSH	SAMPLE	YEAR	DAY	SPECIE	BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.

MARSH SAMPLE DEPTH YEAR DAY SPECIE PM EM ORGANIC MATTER STD. ERR. MEAN

MARSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
EEE	05	76	198	S.ALT	DEAD	184.0		303.3		25.	
EEE	05	76	198	T.DEAD	DEAD	189.0		3.3		9.	
EEE	1	75	95	S.ALT	LIVE	83.1		303.3		73.	
EEE	1	75	149	D.SPI	LIVE			280.0		95.	
EEE	2	75	202	S.ALT	LIVE	365.3		213.0		22.	
EEE	2	75	256	S.ALT	LIVE	862.7		360.0		3.	
EEE	2	75	95	D.SPI	LIVE	708.0		3.3		63.	
EEE	2	75	149	S.ALT	LIVE	51.7		416.7		73.	
EEE	3	75	202	S.ALT	LIVE	.3		250.0		21.	
EEE	3	75	256	S.ALT	LIVE	342.7		210.0		64.	
EEE	3	75	95	S.ALT	LIVE	546.7		436.7		73.	
EEE	3	75	149	S.ALT	LIVE	576.3		196.7		87.	
EEE	3	75	202	S.ALT	LIVE	57.0		260.7		20.	
EEE	4	75	256	S.ALT	LIVE	375.0		300.0		80.	
EEE	4	75	95	S.ALT	LIVE	385.7		260.0		81.	
EEE	4	75	149	S.ALT	LIVE	42.1		203.3		20.	
EEE	4	75	202	S.ALT	LIVE	342.0		376.7		57.	
EEE	4	75	256	S.ALT	LIVE	687.0		10.0		38.	
EEE	5	75	95	S.PAT	LIVE	781.7		303.3		71.	
EEE	5	75	149	D.SPI	LIVE	46.8		56.7		34.	
EEE	5	75	202	D.SPI	LIVE	216.9		293.3		32.	
EEE	5	75	256	D.SPI	LIVE	.7		140.0		35.	
EEE	6	75	95	D.SPI	LIVE	906.7		220.0		21.	
EEE	6	75	149	S.ALT	LIVE	26.3		113.3		18.	
EEE	6	75	202	S.PAT	LIVE	603.7		313.3		42.	
EEE	6	75	202	D.SPI	LIVE	37.2		530.0		38.	
EEE	7	75	256	S.ALT	LIVE	293.3		120.3		35.	
EEE	7	75	95	D.SPI	LIVE	14.3		220.0		70.	
EEE	7	75	149	S.ALT	LIVE	406.7		340.0		20.	
EEE	7	75	202	S.PAT	LIVE	597.3		246.7		45.	
EEE	7	75	256	S.ALT	LIVE	67.3		256.7		11.	
EEE	7	75	95	D.SPI	LIVE	5.3		108.3		24.	
EEE	7	75	149	S.PAT	LIVE	6.2		25.0		26.	
EEE	7	75	202	S.ALT	LIVE	13.0		114.7		46.	
EEE	7	75	202	S.ALT	LIVE	5.0		816.7		31.	
EEE	8	75	256	C.SPI	LIVE	810.3		183.3		46.	
EEE	8	75	256	S.PAT	LIVE	251.7		216.7		31.	
EEE	8	75	95	S.ALT	LIVE	34.2		5883.3		32.	
EEE	8	75	256	D.SPI	LIVE	6.7		16.7		54.	
EEE	8	75	256	S.PAT	LIVE	45.8		141.7		19.	
EEE	8	75	149	S.ALT	LIVE	134.7		8500.0		32.	
EEE					LIVE	6.7		56.3			

MARSH SAMPLE DEPTH YEAR DAY SPICIE NH4 STD. ERR. PO4 STD. ERR. IRON STD. ERR. MN STD. ERR.

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	CA	STD. ERR.	MG	STD. ERR.
BEM	5	10	75	202	SA-SP-DS	391.2	93.4	754.4	150.9
BEM	6	0	75	202	SA-SP-DS	342.6	4.4	616.7	131.8
BEM	6	10	75	202	SA-SP-DS	362.5	11.5	811.8	97.5
BEM	7	0	75	202	SA-SP-DS	267.1	93.6	553.0	600.4
BEM	8	10	75	202	SA-SP-DS	346.2	0.9	811.8	97.3
BEM	9	0	75	202	SP-DS	307.0	49.4	519.3	10.4
BEM	10	10	75	202	SP-DS	435.3	33.3	761.4	222.0
BEM	1	0	75	202	SP-DS	924.7	42.2	870.9	125.4
BEM	1	10	75	202	SP-DS	431.7	9.6	1137.3	144.7
BEM	2	0	75	256	S-ALT	428.3	84.9	860.2	243.8
BEM	2	10	75	256	S-ALT	450.5	72.7	795.5	207.2
BEM	3	0	75	256	S-ALT	418.8	10.8	897.7	25.5
BEM	4	10	75	256	S-ALT	447.5	50.2	1002.1	105.9
BEM	5	0	75	256	S-ALT	431.5	314.3	957.7	55.3
BEM	5	10	75	256	SA-SP-DS	444.7	9.6	973.1	20.4
BEM	6	0	75	256	SA-SP-DS	407.1	42.9	966.0	39.2
BEM	7	10	75	256	SA-SP-GS	338.0	15.6	983.8	83.2
BEM	8	0	75	256	SA-SP-DS	424.3	4.7	995.7	40.0
BEM	8	10	75	256	SA-SP-DS	412.0	93.2	830.0	19.6
BEM	9	0	75	256	SP-DS	383.2	16.0	934.2	283.1
BEM	10	10	75	256	SP-DS	404.7	55.4	883.3	17.1
BEM	10	0	75	256	SP-DS	340.9	44.3	858.6	38.2
BEM	10	10	75	256	SP-DS	448.4	69.2	808.6	71.3
BEM			75	256	SP-DS	435.3	15.3	882.9	53.9
BEM			75	256		935.2	40.6	874.6	65.7
BEM			75	256		496.2	31.7	1046.4	85.0
BEM			75	256		507.4	34.3	1023.2	167.5
BEM							56.9	1218.8	20.7
BEM								1145.4	99.4
BEM								1295.4	43.6
BEM									101.1

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MARSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
BEK		75	149	D-SPI	LIVE	3.3		75.0		14	
BEK		75	149	S-PAT	LIVE	245.8		5250.0		26	
BEK		75	202	S-PAT	LIVE	1083.3		8250.0		50	
BEK		75	256	D-SPI	LIVE	10.0		8.3		31	
BEK		75	256	S-PAT	LIVE	1372.5		9833.3		52	
BEK		75	93	S-PAT	LIVE	13.2		375.0		9	
BEK		75	149	D-SPI	LIVE	59.2		866.7		17	
BEK		75	149	S-ALT	LIVE	250.8		5083.3		25	
BEK		75	202	S-PAT	LIVE	47.5		8.3		90	
BEK		75	202	D-SPI	LIVE	186.7		1056.3		46	
BEK		75	256	S-PAT	LIVE	804.2		6041.7		38	
BEK		75	256	S-PAT	LIVE	920.2		1583.3		36	
BEK		75	93	S-PAT	LIVE	6.9		7160.0		10	
BEK		10	149	S-PAT	LIVE	52.5		191.7		25	
BEK		10	149	S-PAT	LIVE	210.0		616.7		36	
BEK		10	202	S-PAT	LIVE	226.7		5933.3		37	
BEK		10	256	D-SPI	LIVE	780.3		1275.0		45	
BEK		10	256	S-PAT	LIVE	250.0		5033.3			
BEK						946.3		1900.0			
BEK								6500.0			

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MARSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
CB	01	72	231	S.ALT	LIVE	486.0	117.3	180.0			46.0
CB	01	72	231	S.ALT	DEAD	370.3	60.5				
CB	02	72	135	S.ALT	LIVE	135.4	3.0				
CB	02	72	135	S.ALT	DEAD	333.3	14.5				
CB	02	72	231	S.ALT	DEAD	225.9	72.6	246.0			86.0
CB	03	72	231	S.ALT	LIVE	76.0	1.3				
CB	03	72	136	S.PAT	LIVE	118.0	16.7				
CB	03	72	136	T.DEAC	DEAC	499.4	4.7				
CB	03	72	231	S.ALT	LIVE	350.1	167.0	410.0			130.0
CB	03	72	231	D.SPI	LIVE	26.4	20.7	90.0			50.0
CB	03	72	231	T.DEAD	DEAD	141.8	19.4	30.0			870.0
CB	04	72	136	S.ALT	LIVE	175.8	123.2				
CB	04	72	136	S.PAT	LIVE	13.0	98.4				
CB	04	72	231	T.DEAD	DEAD	194.7	4.7				
CB	04	72	231	S.PAT	LIVE	759.7	21.2	780.0			380.0
CB	04	72	231	D.SPI	LIVE	16.4	55.5				
CB	04	72	231	S.PAT	DEAD	552.9	80.0				
CB	04	72	231	T.DEAD	DEAC	285.4	6.3				
CB						310.8					

MARSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
CBR	00	75	148	PMRAG	DEAD	510.2	106.2	190.4	27.2		
CBR	00	75	148	PMRAG	LITTER	308.1	55.0	145.0	8.1		
CBR	00	75	148	PMRAG	LIVE	923.8	24.3				
CBR	00	75	240	S.ALT	LIVE	390.8					
CBR	00	75	240	S.ALT	LITTER	236.0		236.0	14.0	120.	
CBR	01	76	192	S.ALT	LITTER	699.0					
CBR	01	75	192	S.ALT	DEAD	158.0	170.5	234.0	14.0		
CBR	02	75	192	S.ALT	LIVE	892.2	76.1	268.0	24.0	137.	
CBR	02	75	192	S.ALT	DEAD	275.5	693.6				
CBR	02	76	192	S.ALT	DEAD	499.8	107.0	308.0	60.0		
CBR	02	75	192	S.ALT	DEAD	197.5		340.0	50.0	133.	
CBR	02	75	232	S.ALT	DEAD	389.0					
CBR	02	76	232	S.ALT	LIVE	247.0	472.2	210.0	36.0		
CBR	03	75	162	S.ALT	DEAD	339.1	55.1	146.0	24.0	8.	
CBR	03	75	192	S.ALT	DEAC	784.0	27.4	276.0			
CBR	03	74	192	S.ALT	LIVE	86.6		192.0	30.0		
CBR	03	76	232	S.ALT	DEAD	609.0	217.7		80.0		
CBR	04	75	192	S.ALT	DEAD	416.0	1.0	138.0	46.0		
CBR	04	74	232	S.ALT	LIVE	796.5	431.1	210.0	18.0		
CBR	04	76	192	S.ALT	DEAD	28.4	110.4				
CBR	04	76	192	S.ALT	LIVE	345.2		80.0			
CBR	04	74	192	S.ALT	DEAD	238.6		48.0			
CBR	04	76	192	S.ALT	DEAD	329.0	210.8	330.0			
CBR	04	76	232	S.ALT	DEAD	505.7	23.8				
CBR	04	75	232	S.ALT	DEAD	65.4	12.6				
CBR	05	76	162	D.SPI	LIVE	30.4	2.6				
CBR	05	75	192	SCIR	LIVE	40.5	1251.2				
CBR	05	75	192	T.GEAD	DEAD	245.1	597.C				
CBR	05	75	232	S.ALT	DEAD	30.8	12.3				

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MARSH SAMPLE DEPTH YEAR DAY SPECIE PH EH ORGANIC MATTER STD. ERR. MEAN

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	PH	EH	ORGANIC MATTER	STD. ERR. MEAN
CRA	01	0	75	102	SALT	6.72	-320		
CRA	02	10	75	102	SALT	7.2	-280		
CRA	02	0	75	102	SALT	5.22	-90		
CRA	03	10	75	102	SALT	6.33	-205		
CRA	04	0	75	102	SALT	7.03	-170		
CRA	05	10	75	102	SCIR	6.7	-240		
CRA	05	10	75	102	SCIR	6.3	120		

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	NH4	STD. ERR.	PO4	STD. ERR.	IRON	STD. ERR.	MN	STD. ERR.
C8S1	01	0	75	162	S.ALT	8.33							
C8S1	01	10	75	162	S.ALT	4.50							
C8S1	02	0	75	162	S.ALT	11.00							
C8S1	04	10	75	162	S.ALT	6.90							
C8S1	05	0	75	162	S.ALT	14.30							
C8S1	05	10	75	162	SCIR	7.15							
						14.85							

MARSH	SAMPLE	YEAR	DAY	SPECIES		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
FIS	01	75	238	SALIC	LIVE	182.2	10.9	88.0	16.0		
FIS	02	75	238	S.ALT	LIVE	1453.0	26.2	52.0	12.0		
FIS	02	75	238	S.DIG	LIVE	1114.6	30.2	832.0	32.0		
FIS	02	75	238	T.DEAD	DEAD	24.8	4.2				
FIS	02	75	238	UNK	LIVE	14.0	1.2				
FIS	03	75	238	S.ALT	LIVE	2112.0	44.8	38.0	10.0		
FIS	03	75	238	S.DIG	LIVE	486.0	27.6	32.0	28.0		
FIS	03	75	238	T.DEAD	DEAD	8.1	4.0	100.0	400.0		
FIS	03	75	238	UNK	LIVE	22.4	5.7				
FIS	05	75	238	D.SPI	LIVE	0.2	956.0	50.0	14.0		
FIS	05	75	238	S.PAT	LIVE	3224.0	44.5	24.0	24.0		
FIS	05	75	238	PHRAG	LIVE	1453.0					
FIS	05	75	238	T.DEAD	DEAD	171.4	1.4				

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MARSH SAMPLE DEPTH YEAR DAY SPECIE PM EM ORGANIC MATTER STD. ERR. MEAN

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	NH4	STD. ERR.	PO4	STD. ERR.	IRON	STD. ERR.	MN	STD. ERR.
PIS	03	0	75	109	S:ALT	2.20		42.9	7.2	64.2			
PIS	03	10	75	109	S:ALT	9.88		46.3	3.4	11.7			
PIS	03	10	75	109	SP-OS	2.00		30.7					
						1.90							

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MARSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
FGL	01	75	170	S.ALT	LIVE			152.0		152.0	
FGL	01	75	170	S.ALT	DEAD			572.0		128.0	
FGL	02	75	170	S.ALT	LIVE			32.0		12.0	
FGL	03	75	170	S.ALT	DEAD			404.0			
FGL	03	75	170	D.SPI	LIVE						
FGL	03	75	170	T.DEAD	DEAD						
FGL	04	75	170	S.SPI	LIVE			202.0		10.0	
FGL	04	75	170	PHRAG	LIVE			142.0		22.0	
FGL	04	75	230	T.DEAD	DEAD						
FGL	04	75	230	PHRAG	DEAD			22.0		6.0	
FGL	05	75	170	PHRAG	LIVE			25.0		25.0	
FGL	05	75	170	PHRAG	LITTER			82.0		82.0	
FGL	05	75	230	PHRAG	LIVE						
FGL	05	75	230	PHRAG	DEAD			40.0		12.0	
FGL	05	75	230	PHRAG	LITTER						

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MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	NH4	STD. ERR.	PO4	STD. ERR.	IRON	STD. ERR.	MN	STD. ERR.
FO6	02	10	75	170	S.ALT			95.0		144.7			
FO6	02	0	75	170	S.ALT			4.9		90.3			
FO6	02	20	75	170	S.ALT			21.0		85.0			
FO6	033	0	75	170	S.ALT	3.83		10.8		106.0			
FO6	04	10	75	170	SA-DS	2.48		21.1		9.8			
FO6	044	0	75	170	SA-SP-DS	3.55		322.5		26.1			
FO6	05	10	75	170	SA-SP-DS	4.68		12.3		92.1			
FO1	05		75	170	PHRAG	2.15		12.5		15.7			
					PHRAG	2.20		260.0		61.9			
								19.0		76.0			

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MARSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
G&S	01	75	171	S.ALT	LIVE	270.6	72.1	610.0	34.0		
G&S	01	75	171	S.ALT	DEAD	113.9	4.5	478.0	85.0		
G&S	01	75	238	S.ALT	LIVE	527.2	10.6				
G&S	02	75	171	S.ALT	DEAD	37.0	16.8	132.0	72.0		
G&S	02	75	171	S.ALT	DEAD	322.6	36.8				
G&S	02	75	171	SALIC	LIVE	314.4					
G&S	02	75	238	T.CEAD	DEAD	1.4	32.0				
G&S	02	75	238	S.ALT	LIVE	197.0	72.6	71.0	97.0		
G&S	02	75	238	S.BIG	DEAD	260.8	16.0				
G&S	03	75	171	T.DEAC	LIVE	377.6	50.0				
G&S	03	75	171	S.ALT	LIVE	6.6					
G&S	03	75	238	SALIC	DEAD	9.0	.4				
G&S	04	75	171	T.DEAD	DEAD	86.1	80.0	356.0	356.0		
G&S	04	75	171	SALIC	LIVE	293.6	71.5	116.0	116.0		
G&S	04	75	171	SALIC	LIVE	23.7	15.4				
G&S	04	75	238	T.CEAD	DEAD	222.8	20.8				
G&S	04	75	238	LITT	LIVE	96.4					
G&S	05	75	171	S.ALT	DEAD	335.6	4.3	730.0	102.0		
G&S	05	75	171	S.ALT	LIVE	135.6	.1				
G&S	05	75	171	D.SPI	LIVE	51.4	16.0	170.0	10.0		
G&S	05	75	238	SALIC	LIVE	174.4	90.6	380.0	40.0		
G&S	05	75	238	T.DEAD	DEAD	2.6					
G&S	05	75	238	S.ALT	DEAD	254.3	104.3	40.0	246.0		
G&S	05	75	238	D.SPI	LIVE	90.9	5.4	772.0	130.0		
G&S	05	75	238	S.PAT	LIVE	132.1	32.8	224.0			
G&S	05	75	238	T.CEAD	DEAD	101.1	7.7				

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MARSH SAMPLE DEPTH YEAR DAY SPECIE PH EH ORGANIC MATTER STD. ERR. MEAN

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	NH4	STD. ERR.	PO4	STD. ERR.	IRON	STD. ERR.	NH	STD. ERR.
GAR	01	0	75	171	S.ALT	2.02		159.1		353.0			
G38	01	10	75	171	S.ALT	3.03		226.9		35.4			
G38	01	20	75	171	S.ALT	3.50		160.0		25.1			
G38	02	0	75	171	S.ALT	6.88		232.0					
G38	03	10	75	171	S.ALT	27.50		196.2		382.8			
G38	03	0	75	171	SALIC	8.80		30.3		126.2			
G38	06	10	75	171	SALIC	4.13				74.9			
G38	06	0	75	171	S.ALT	9.23		31.1		31.8			
G38	05	10	75	171	SA-OS	2.60		46.3		15.8			
G38	05	0	75	171	SA-OS	2.03		6.8		31.6			
G38	05	20	75	171	SA-OS	7.43		162.5		11.8			
								47.4		23.0			

MARSH SAMPLE YEAR DAY SPECIE BIOMASS STD. ERR. STEM DENSITY STD. ERR. STEM WT. STD. ERR.

MARSH SAMPLE DEPTH YEAR DAY SPECIE PH EH ORGANIC MATTER STD. ERR. MEAN

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	CA	STD. ERR.	MG	STD. ERR.
	06	0	75	101	SA-DS			945.	
	06	10	75	101	SA-DS			712.	
	06	20	75	101	SA-DS			1052.	
	07	0	75	101	SA-DS			980.	
	07	10	75	101	S-ALT			1016.	
	07	20	75	101	SA-SP-DS			683.	
	08	0	75	101	SA-SP-DS			700.	
	08	10	75	101	SA-DS			605.	
	08	20	75	101	SA-DS			802.	
	09	30	75	101	SA-DS			700.	
	11	0	75	101	SA-SP-DS			615.	
	11	20	75	101	SA-SP-DS			700.	
	11	30	75	101	SA-SP-DS			856.	
	11	0	75	101	T-DEAD			760.	
	11	10	75	101	T-DEAD			730.	
	12	20	75	101	SA-SP-DS			734.	
	12	30	75	101	SP-DS			1016.	
	12	0	75	101	SP-DS			772.	
	12	0	75	101	SP-DS			1037.	
		0	75	101	PHRAG			4.	
		0	75	101	PHRAG			345.	
		0	75	101	PHRAG			251.	
		0	75	101	PHRAG			1231.	
		0	75	101	PHRAG			345.	
		0	75	101	PHRAG			925.	
		0	75	101	PHRAG			925.	
		0	75	101	PHRAG			925.	
		0	75	101	PHRAG			760.	
		0	75	101	PHRAG			34.	
		0	75	101	PHRAG			925.	

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RADN SAMPLE YEAR DAY SPECIE BIOMASS STD. ERR. STEM DENSITY STD. ERR. STEM WT. STD. ERR.

MARSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
LYE	17	75	237	PHRAG	LIVE	478.8	315.8				
LYE	17	75	237	PHRAG	DEAD	335.0	21.7	74.0	2.0		
LYE	17	75	237	PHRAG	LITTER	724.9	103.3				
LYE	18	75	101	PHRAG	LIVE	169.3	76.1	36.0	12.0		
LYE	18	75	101	PHRAG	DEAD	598.0	180.6	72.0	36.0		
LYE	18	75	237	PHRAG	LIVE	594.7	31.7	84.0			
LYE	18	75	237	PHRAG	LITTER	165.0	85.6				

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MARSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
PGR	01	75	231	S.ALT	LIVE	660.6	6.2	190.0	22.0		
PGR	02	75	231	S.ALT	DEAD	221.3	31.8	254.0	26.0		
PGR	02	75	231	S.ALT	LIVE	111.0	18.9				
PGR	03	75	231	D.SPI	LIVE	401.3	1623	210.0	490.0		

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MARSH SAMPLE DEPTH YEAR DAY SPECIE PH EH ORGANIC MATTER STD. ERR. MEAN

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	NH4	STD. ERR.	PO4	STD. ERR.	IRON	STD. ERR.	PH	STD. ERR.
PCB	01	0	75	156	S.ALT			904	23.3				
PCB	01	10	75	156	S.ALT			273	3.5				
PCB	01	20	75	156	S.ALT			220	6.2				
PCB	02	30	75	156	S.ALT			106	6.7				
PCB	02	10	75	156	S.ALT			34.5	8.7				
PCB	02	20	75	156	S.ALT			34.6		137.7			
PCB	02	30	75	156	D.SPI			49.8	20.2				
PCB	03	0	75	156	D.SPI			828	20.2				
PCB	03	10	75	156	D.SPI			41.9	19.0				
PCB	03	20	75	156	D.SPI			711	0.9				
PCB	03	30	75	156				011					

MARSH SAMPLE YEAR DAY SPECIE BIOMASS STD. ERR. STEM DENSITY STD. ERR. STEM WT. STD. ERR.

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	PM	EM	ORGANIC MATTER	STD. ERR.	MEAN
SAP	11	0	72	202	SA-DS					
SAP	11	10	72	202	SA-DS					
SAP	11	20	72	202	SA-DS					
SAP	11	30	72	202	SA-DS					
SAP	22	0	72	202	S.ALT					
SAP	22	10	72	202	S.ALT					
SAP	22	20	72	202	S.ALT					
SAP	22	40	72	202	S.ALT					
SAP	33	0	72	202	J.ROM					
SAP	33	20	72	202	J.ROM					
SAP	33	40	72	202	J.ROM					
SAP	44	10	72	202	S.ALT					
SAP	44	30	72	202	S.ALT					

MARSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
005	01	75	171	S.ALT	LIVE	311.1	10.0	648.0		108.0	
005	01	75	171	S.ALT	DEAD	226.0	16.2				
005	01	75	239	S.ALT	DEAD	225.9					
005	01	75	171	S.ALT	LIVE	450.3	320.0				
005	02	75	171	D.SPI	LIVE	7.6	.3	6.0		166.0	
005	02	75	171	T.DEAD	DEAD	648	8.33	830.0			
005	02	75	239	D.SPI	DEAD	1303	202.6				
005	02	75	239	D.SPI	LIVE	60.0	61.1	196.0		220.0	
005	03	75	171	T.LDEAD	DEAD	403.4	61.8	660.0		205.0	
005	03	75	171	J.ROM	LIVE	10.8	643				
005	03	75	171	J.ROM	DEAD	203.7	60.5				

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MARSH SAMPLE DEPTH YEAR DAY SPECIE PH EH ORGANIC MATTER STD. ERR. MEAN

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	PH	EH	ORGANIC MATTER	STD. ERR. MEAN
003	01	0	77	171	S.ALT		90	98.0	
003	01	0	77	171	S.ALT		-250	60.3	
003	01	20	77	171	S.ALT		-350		
003	02	0	77	171	SA-OS		-100		
003	02	20	77	171	SA-OS		-300		
003	03	0	77	171	SA-OS		-200		
003	03	20	77	171	J.ROM		90		
003	03	20	77	171	J.ROM		170		
003	03		77	171	J.ROM		125		

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	NH4	STD. ERR.	PO4	STD. ERR.	IRON	STD. ERR.	MN	STD. ERR.
005	01	0	75	171	S.ALT	10.43		30.4	10.5	34.7			
005	01	10	75	171	S.ALT	3.38		62.1		3.2			
005	01	20	75	171	S.ALT	10.73		4.0		62.0			
005	03	0	75	171	J.ROM	7.13		4.0		92.3			
005	03	10	75	171	J.ROM	11.55		27.1		6.5			
005	03	20	75	171	J.ROM	2.20		9.6	80.0	15.2			
005	02	0	75	171	SA-DS	1.38		9.7		9.8			
005	02	10	75	171	SA-DS	15.13		4.3		13.0			
005	02	20	75	171	SA-DS	4.13		17.3		45.9			
005	02	30	75	171	SA-DS	10.45		3.8		103.5			
005	02		75	171	SA-DS	17.33							

MARSH SAMPLE YEAR DAY SPECIE BIOMASS STD. ERR. STEM DENSITY STD. ERR. STEM WT. STD. ERR.

MARSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
TAS	01	76	126	S.ALT	LIVE	198.0				80.	
TAS	01	76	126	S.ALT	DEAD	319.4					
TAS	01	76	126	S.EUR	LIVE	320.6		100.0		65.	
TAS	01	76	158	S.EUR	DEAD	240.7		76.0		35.	
TAS	01	76	158	S.ALT	LIVE	392.1		194.0		27.	
TAS	01	76	238	S.ALT	DEAD	417.0		260.0			
TAS	02	76	126	S.ALT	LIVE	77.0					
TAS	02	76	238	S.ALT	DEAD	76.4				48.	
TAS	02	76	238	D.SPI	LIVE	260.1		287.5		44.	
TAS	02	76	238	J.GER	LIVE	186.0		500.0			
TAS	03	76	126	D.SPI	LIVE	4.35	82.0	184.0			
TAS	03	76	238	S.PAT	LIVE	311.0	75.0	140.0			
TAS	03	76	124	T.DEAD	DEAD	132.0	73.0			100.	
TAS	06	76	238	D.SPI	LIVE	33.3					
TAS	06	76	183	S.PAT	LIVE	55.4				100.	
TAS	06	76	183	D.SPI	LIVE	154.0				44.	
TAS	06	76	183	S.ALT	LIVE	461.0		700.0	8.0		
TAS	06	76	183	T.DEAD	DEAD	7.4	44.0	40.0	16.0		
TAS	09	76	164	S.ALT	LIVE	360.6				680.	
TAS	09	76	164	S.ALT	DEAD	337.6				60.	
TAS	09	76	238	S.ALT	LIVE	406.1		94.0			
TAS	09	76	238	S.ALT	DEAD	425.1				400.	
TAS	11	76	238	S.ALT	LIVE	7.2		938.0			
TAS	11	76	164	T.DEAD	DEAD	292.1	131.0				
TAS	11	76	238	S.PAT	DEAD	457.0	272.0			54.	
TAS	12	76	238	S.ALT	LIVE	875.0				222.	
TAS	13	76	238	S.ALT	DEAD	80.0					
TAS	13	76	164	S.PAT	LIVE	91.0				200.	
TAS	13	76	164	S.ALT	LITTER	923.0					
TAS	13	76	238	S.PAT	LIVE	970.0					
TAS	13	76	238	S.ALT	DEAD	235.0					
TAS	13	76	164	S.PAT	LIVE	243.0					
TAS	13	76	164	T.DEAD	DEAD	600.0					
TAS	13	76	164	D.SPI	LITTER	132.0					
TAS	13	76	164	S.PAT	LITTER	11.0					
TAS	13	76	164	SCIR	LITTER						
TAS	21	76	238	SCIR	LITTER	192.0		401.0			
TAS	21	76	164	T.DEAD	LIVE	80.0		112.0			
TAS	21	76	164	D.SPI	DEAD	321.7					
TAS	22	76	238	T.DEAD	DEAD	273.0					
TAS	22	76	164	S.ALT	LIVE	657.0		960.0			
TAS	22	76	164	S.ALT	LITTER	161.0					
TAS	22	76	164	D.SPI	DEAD	292.0					

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MARSH SAMPLE DEPTH YEAR DAY SPECIE ZA STD. ERR. MG STD. ERR. STD. ERR.

MRSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
TAS	22	74	186	S.PAT	LIVE	565.0				720.	
TAS	22	74	186	S.PAT	DEAD	370.0				300.	
TAS	23	74	186	S.PAT	LITTER	32.0					
TAS	23	74	186	D.SPI	LITTER	205.0				120.	
TAS	23	74	186	S.PAT	LIVE	107.0				240.	
TAS	23	74	186	S.PAT	LITTER	53.0					
TAS	23	74	186	SCIR	LIVE	113.0					
TAS	23	74	186	SCIR	LITTER	69.0		192.0		170.	
TAS	31	74	186	T.DEAD	DEAD	444.0					
TAS	31	74	186	S.ALT	DEAD	432.0				256.	
TAS	31	74	186	S.ALT	LITTER	413.0		200.0			
TAS	32	74	186	D.SPI	LIVE	30.0					
TAS	32	74	186	D.SPI	DEAD	35.0				800.	
TAS	32	74	186	S.PAT	LIVE	391.0		720.0			
TAS	32	74	186	D.SPI	DEAD	40.0					
TAS	33	74	186	D.SPI	LIVE	225.0				260.	
TAS	33	74	186	S.PAT	LITTER	83.0				420.	
TAS	33	74	186	SCIR	LITTER	57.0				260.	
TAS	33	74	186	T.DEAD	DEAD	146.0		46.7		30.	
TAS	33	1	202	S.ALT	LIVE	82.0		653.3		80.	
TAS	1	75	202	S.ALT	LIVE	456.3		133.3		97.	
TAS	1	75	95	S.ALT	LIVE	115.0		126.7		121.	
TAS	2	75	149	S.ALT	LIVE	627.3		166.7		22.	
TAS	2	75	202	S.ALT	LIVE	80.7		70.0		55.	
TAS	2	75	236	S.ALT	LIVE	39.3		70.0		71.	
TAS	2	75	95	S.ALT	LIVE	77.0		100.0		86.	
TAS	3	75	202	S.PAT	LIVE	292.0		80.0		17.	
TAS	3	75	236	S.ALT	LIVE	364.3		90.0		6.	
TAS	3	75	95	S.PAT	LIVE	7.4		6.7		46.	
TAS	3	75	149	S.ALT	LIVE	111.7		133.3		21.	
TAS	3	75	149	S.PAT	LIVE	6.7		90.0		65.	
TAS	4	75	202	S.PAT	LIVE	27.3		200.0		37.	
TAS	4	75	202	D.SPI	LIVE	458.3		26.7		65.	
TAS	4	75	236	S.ALT	LIVE	10.0		186.7		61.	
TAS	4	75	236	D.SPI	LIVE	418.7		376.7		36.	
TAS	4	75	236	S.PAT	LIVE	7.3		46.7		21.	
TAS	4	75	95	S.ALT	LIVE	6.7		36.3		40.	
TAS	4	75	149	S.PAT	LIVE	50.0		186.3		21.	
TAS	4	75	149	D.SPI	LIVE	32.3		175.0		25.	
TAS	4	75	149	S.PAT	LIVE	85.0		1241.7		30.	

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MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	CA	STD. ERR.	MG	STD. ERR.
TAS	1	10	72	250	S.ALT	422.8	31.0	841.1	27.7
TAS	2	10	72	250	S.ALT	442.8	49.0	804.1	51.3
TAS	2	10	72	250	S.ALT	441.1	35.1	925.0	37.0
TAS	3	10	72	250	SA-SP-DS	313.7	47.1	826.3	45.1
TAS	4	10	72	250	SA-SP-DS	406.0	133.3	1140.9	35.7
TAS	5	10	72	250	SA-SP-DS	446.5	133.3	924.0	175.5
TAS	6	10	72	250	SA-SP-DS	361.7	150.2	1115.9	204.0
TAS	6	10	72	250	SA-SP-DS	400.3	82.0	865.7	281.6
TAS	7	10	72	250	SP-DS	352.0	44.8	1176.7	227.6
TAS	7	10	72	250	SP-DS	331.5	44.8	855.4	133.6
TAS	8	10	72	250	SP-DS	452.7	68.1	1116.7	120.4
TAS	8	10	72	250	SP-DS	335.5	37.7	1060.6	25.7
TAS	8	10	72	250	SP-DS	442.4	92.6	766.7	21.6
TAS		10	72	250				1007.1	36.9

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MARSH  SAMPLE  YEAR    DAY        SPECIE             BIOMASS    STD. ERR.    STEM DENSITY    STD. ERRR.    STEM HT.    STD. ERR.
••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••••

 TAS      4      75    202    S.ALT   LIVE           377.5                   183.3                       61.
 TAS      4      75    202    D.SPI   LIVE            97.5                   700.0                       38.
 TAS      4      75    202    S.PAT   LIVE           214.2                   991.7                       40.
 TAS      4      75    256    S.ALT   LIVE           323.3                   100.0                       74.
 TAS      4      75    256    D.SPI   LIVE           283.3                  1466.7                       43.
 TAS      4      75    256    S.PAT   LIVE           383.3                  1683.3                       43.
 TAS      5      75     95    S.ALT   LIVE             1.2                     8.3                       19.
 TAS      5      75     95    D.SPI   LIVE              .3                     8.3                        8.
 TAS      5      75     95    S.PAT   LIVE            19.7                   275.0                       21.
 TAS      5      75    149    D.SPI   LIVE            57.5                   675.0                       23.
 TAS      5      75    149    S.PAT   LIVE            47.5                   625.0                       26.
 TAS      5      75    202    S.ALT   LIVE            13.3                    25.0                       42.
 TAS      5      75    202    D.SPI   LIVE           330.0                  2175.0                       34.
 TAS      5      75    202    S.PAT   LIVE           333.3                  1925.0                       39.
 TAS      5      75    256    D.SPI   LIVE           259.3                  1341.7                       44.
 TAS      5      75    256    S.PAT   LIVE           840.8                  3083.3                       48.
 TAS      6      75     95    S.PAT   LIVE            49.2                   658.3                       17.
 TAS      6      75    149    D.SPI   LIVE            50.0                   533.3                       24.
 TAS      6      75    149    S.PAT   LIVE           140.8                  1200.0                       34.
 TAS      6      75    202    D.SPI   LIVE           256.7                  1250.0                       42.
 TAS      6      75    202    S.PAT   LIVE          1153.3                  5583.3                       47.
 TAS      6      75    256    D.SPI   LIVE           344.2                  1450.0                       46.
 TAS      6      75    256    S.PAT   LIVE           637.5                  2241.7                       50.
 TAS      7      75     95    S.PAT   LIVE            97.6                  1125.0                       21.
 TAS      7      75    149    D.SPI   LIVE            45.8                   533.3                       30.
 TAS      7      75    149    S.PAT   LIVE           207.5                  2183.3                       30.
 TAS      7      75    202    D.SPI   LIVE            75.8                   425.0                       40.
 TAS      7      75    202    S.PAT   LIVE           705.8                  2616.7                       48.
 TAS      7      75    256    D.SPI   LIVE            78.3                   341.7                       43.
 TAS      7      75    256    S.PAT   LIVE           870.0                  3750.0                       50.
 TAS      8      75     95    D.SPI   LIVE             1.0                    16.7                        9.
 TAS      8      75     95    S.PAT   LIVE            25.6                   325.0                       24.
 TAS      8      75    149    D.SPI   LIVE            57.5                   783.3                       25.
 TAS      8      75    149    S.PAT   LIVE           209.2                  2875.0                       32.
 TAS      8      75    202    D.SPI   LIVE           215.0                  1700.0                       39.
 TAS      8      75    202    S.PAT   LIVE           239.2                  1200.0                       45.
 TAS      8      75    256    D.SPI   LIVE           570.8                  2058.3                       44.
 TAS      8      75    256    S.PAT   LIVE           255.8                  2566.7                       48.
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MARSH	SAMPLE	YEAR	DAY	SPECIE		BIOMASS	STD. ERR.	STEM DENSITY	STD. ERR.	STEM WT.	STD. ERR.
1	01	75	238	S.ALT	LIVE	400.2	29.8	348.0	28.0		
1	01	75	170	S.ALT	LIVE	315.2	50.5	470.0	50.0		
1	01	75	238	S.ALT	DEAD	330.1	190.8				
1	02	75	170	S.ALT	LIVE	192.5	48.4	144.0	16.0		
1	02	75	170	S.ALT	LIVE	330.1	28.6				
1	03	75	238	S.ALT	DEAD	372.7	16.0	782.0	674.0		
1	03	75	238	S.ALT	LIVE	50.5	3.7	244.0	46.0		
1	03	75	238	SALIC	LIVE	126.8	.9				
1	03	75	238	T.DEAD	DEAD	165.2	101.4	380.0	220.0		
1	03	75	238	S.ALT	DEAD	39.8	6.8				
1	06	75	170	S.ALT	LIVE	155.0	50.1				
1	06	75	170	SALIC	DEAD	481.9	500.0				
1	06	75	170	S.ALT	LIVE	204.7	95.3	290.0	10.0		
1	06	75	170	D.SPI	LIVE	100.1	30.1	50.0	90.0		
1	07	75	170	SALIC	LIVE	31.8	240.0				
1	07	75	170	T.DEAD	DEAD	367.7	41.7	630.0	290.0		
1	07	75	170	D.SPI	LIVE	221.9	13.1	510.0	210.0		
1	07	75	170	SALIC	LIVE	255.2	20.7				
1	07	75	170	T.DEAD	DEAD	241.8	5.8				

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	PH	EH	ORGANIC MATTER	STD. ERR. MEAN
WAL	01	0	75	170	S.ALT	5.9	-400	11.1	
WAL	01	10	75	170	S.ALT	6.4	-350	11.4	
WAL	01	20	75	170	S.ALT	6.3	-350	9.1	
WAL	01	30	75	170	S.ALT	6.5	-330	9.0	
WAL	02	0	75	170	S.ALT	6.6	-330	17.1	
WAL	02	10	75	170	S.ALT	6.2	-205	6.2	
WAL	02	20	75	170	S.ALT	6.5	-350	11.2	
WAL	02	30	75	170	S.ALT	6.7	-340	9.9	
WAL	02	40	75	170	S.ALT	6.5	-330		
WAL	02	50	75	170	S.ALT	6.5	-340		
WAL	02	60	75	170	S.ALT	6.5	-310		
WAL	03	0	75	170	SALIC	5.9	-130	8.0	
WAL	03	10	75	170	SALIC	6.6	-70	5.6	
WAL	03	20	75	170	SALIC	6.2	-270	18.5	
WAL	03	30	75	170	SALIC	6.4	-345	11.0	
WAL	03	40	75	170	SALIC	6.5	-345		
WAL	03	50	75	170	SALIC	6.7	-345		
WAL	03	60	75	170	SALIC	6.7	-345		
WAL	04	0	75	170	S.ALT	6.4	190	3.3	
WAL	04	10	75	170	S.ALT	5.4	190	2.9	
WAL	04	20	75	170	S.ALT	5.6	180	3.4	
WAL	04	30	75	170	S.ALT	6.9	-325	10.5	
WAL	04	40	75	170	S.ALT	6.7	-335		
WAL	05	0	75	170	SALIC	6.4	140	4.8	
WAL	05	10	75	170	SALIC	6.6	155	2.4	
WAL	05	20	75	170	SALIC	6.9	-295	9.3	
WAL	05	30	75	170	SALIC	6.3	-260		
WAL	06	0	75	170	SA-DS	6.3	30	4.0	.5
WAL	06	10	75	170	SA-DS	6.3	220		
WAL	06	20	75	170	SA-DS	6.5	120	1.5	
WAL	07	0	75	170	D.SPI	6.6		6.8	
WAL	07	10	75	170	D.SPI	6.5	60	7.5	
WAL	07	20	75	170	D.SPI	6.5	120	5.6	

MARSH	SAMPLE	DEPTH	YEAR	DAY	SPECIE	MN4	STD. ERR.	PO4	STD. ERR.	IRON	STD. ERR.	MN	STD. ERR.
M41	01	0	75	170	S-ALT	9.23		44.9		443.9			
M41	01	10	75	170	S-ALT	2.50		40.2		138.4			
M41	01	20	75	170	S-ALT	4.13		35.8		116.5			
M41	01	30	75	170	S-ALT			44.0		115.5			
M41	02	0	75	170	S-ALT	10.73		192.2		980.7			
M41	02	10	75	170	S-ALT	1.93		9.2		2303.7			
M41	02	20	75	170	S-ALT	1.38		27.8		1206.0			
M41	03	0	75	170	S-ALT	3.03		44.9		123.3			
M41	03	10	75	170	SALIC	1.35		127.0		116.1			
M41	03	20	75	170	SALIC	2.75		102.2		143.4			
M41	04	0	75	170	SALIC	1.05		28.1		185.5			
M41	04	10	75	170	SALIC	7.70		306.9		184.0			
M41	04	20	75	170	S-ALT	2.30		165.4		225.7			
M41	05	0	75	170	S-ALT	1.45		112.0		119.2			
M41	05	30	75	170	SALIC	3.30		146.9		110.5			
M41	06	10	75	170	SALIC	3.85	10.8	328.2		104.6		45.9	
M41	06	20	75	170	SA-DS	2.55	1.4	26.2		440.6		72.9	
M41	07	0	75	170	SA-DS	1.90		118.8		350.1			
M41	07	10	75	170	D-SPI	1.92		236.2		286.2			
M41	07	20	75	170	D-SPI	3.30		92.0		51.0			
M41	07	30	75	170	D-SPI	2.75		37.1		75.2			
M41			75	170				211.4		25.0			
M41			75	170		1.38		19.3		95.3			
M41			75	170				18.7		23.9			
M41			75	170		1.50		27.7		17.3			
M41			75	170				127.7		66.8			